DARWINISM

AN EXPOSITION OF THE

THEORY OF NATURAL SELECTION

WITH SOME OF ITS APPLICATIONS

BY

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WITH A PORTRAIT OF THE AUTHOR, MAP AND ILLUSTRATIONS

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[Illustration: Alfred R. Wallace]

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PREFACE TO SECOND EDITION

The present edition is a reprint of the first, with a few verbal

corrections and the alteration of some erroneous or doubtful statements.

Of these latter the following are the most important:--

\_P.\_ 30. The statement as to the fulmar petrel, which Professor A.

Newton assures me is erroneous, has been modified.

\_P.\_ 34. A note is added as to Darwin's statement about the missel and

song-thrushes in Scotland.

\_P.\_ 172. An error as to the differently-coloured herds of cattle in the

Falkland Islands, is corrected.

PARKSTONE, DORSET

\_August, 1889\_.

PREFACE TO FIRST EDITION

The present work treats the problem of the Origin of Species on the same

general lines as were adopted by Darwin; but from the standpoint reached

after nearly thirty years of discussion, with an abundance of new facts

and the advocacy of many new or old theories.

While not attempting to deal, even in outline, with the vast subject of

evolution in general, an endeavour has been made to give such an account

of the theory of Natural Selection as may enable any intelligent reader

to obtain a clear conception of Darwin's work, and to understand

something of the power and range of his great principle.

Darwin wrote for a generation which had not accepted evolution, and

which poured contempt on those who upheld the derivation of species from

species by any natural law of descent. He did his work so well that

"descent with modification" is now universally accepted as the order of

nature in the organic world; and the rising generation of naturalists

can hardly realise the novelty of this idea, or that their fathers

considered it a scientific heresy to be condemned rather than seriously

discussed.

The objections now made to Darwin's theory apply, solely, to the

particular means by which the change of species has been brought about,

not to the fact of that change. The objectors seek to minimise the

agency of natural selection and to subordinate it to laws of variation,

of use and disuse, of intelligence, and of heredity. These views and

objections are urged with much force and more confidence, and for the

most part by the modern school of laboratory naturalists, to whom the

peculiarities and distinctions of species, as such, their distribution

and their affinities, have little interest as compared with the problems

of histology and embryology, of physiology and morphology. Their work in

these departments is of the greatest interest and of the highest

importance, but it is not the kind of work which, by itself, enables one

to form a sound judgment on the questions involved in the action of the

law of natural selection. These rest mainly on the external and vital

relations of species to species in a state of nature--on what has been

well termed by Semper the "physiology of organisms," rather than on the

anatomy or physiology of organs.

\* \* \* \* \*

It has always been considered a weakness in Darwin's work that he based

his theory, primarily, on the evidence of variation in domesticated

animals and cultivated plants. I have endeavoured to secure a firm

foundation for the theory in the variations of organisms in a state of

nature; and as the exact amount and precise character of these

variations is of paramount importance in the numerous problems that

arise when we apply the theory to explain the facts of nature, I have

endeavoured, by means of a series of diagrams, to exhibit to the eye the

actual variations as they are found to exist in a sufficient number of

species. By doing this, not only does the reader obtain a better and

more precise idea of variation than can be given by any number of

tabular statements or cases of extreme individual variation, but we

obtain a basis of fact by which to test the statements and objections

usually put forth on the subject of specific variability; and it will be

found that, throughout the work, I have frequently to appeal to these

diagrams and the facts they illustrate, just as Darwin was accustomed to

appeal to the facts of variation among dogs and pigeons.

I have also made what appears to me an important change in the

arrangement of the subject. Instead of treating first the comparatively

difficult and unfamiliar details of variation, I commence with the

Struggle for Existence, which is really the fundamental phenomenon on

which natural selection depends, while the particular facts which

illustrate it are comparatively familiar and very interesting. It has

the further advantage that, after discussing variation and the effects

of artificial selection, we proceed at once to explain how natural

selection acts.

Among the subjects of novelty or interest discussed in this volume, and

which have important bearings on the theory of natural selection, are:

(1) A proof that all \_specific\_ characters are (or once have been)

either useful in themselves or correlated with useful characters (Chap.

VI); (2) a proof that natural selection can, in certain cases, increase

the sterility of crosses (Chap. VII); (3) a fuller discussion of the

colour relations of animals, with additional facts and arguments on the

origin of sexual differences of colour (Chaps. VIII-X); (4) an attempted

solution of the difficulty presented by the occurrence of both very

simple and very complex modes of securing the cross-fertilisation of

plants (Chap. XI); (5) some fresh facts and arguments on the

wind-carriage of seeds, and its bearing on the wide dispersal of many

arctic and alpine plants (Chap. XII); (6) some new illustrations of the

non-heredity of acquired characters, and a proof that the effects of use

and disuse, even if inherited, must be overpowered by natural selection

(Chap. XIV); and (7) a new argument as to the nature and origin of the

moral and intellectual faculties of man (Chap. XV).

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Although I maintain, and even enforce, my differences from some of

Darwin's views, my whole work tends forcibly to illustrate the

overwhelming importance of Natural Selection over all other agencies in

the production of new species. I thus take up Darwin's earlier

position, from which he somewhat receded in the later editions of his

works, on account of criticisms and objections which I have endeavoured

to show are unsound. Even in rejecting that phase of sexual selection

depending on female choice, I insist on the greater efficacy of natural

selection. This is pre-eminently the Darwinian doctrine, and I therefore

claim for my book the position of being the advocate of pure Darwinism.

I wish to express my obligation to Mr. Francis Darwin for lending me

some of his father's unused notes, and to many other friends for facts

or information, which have, I believe, been acknowledged either in the

text or footnotes. Mr. James Sime has kindly read over the proofs and

given me many useful suggestions; and I have to thank Professor Meldola,

Mr. Hemsley, and Mr. E.B. Poulton for valuable notes or corrections in

the later chapters in which their special subjects are touched upon.

GODALMING, \_March 1889\_.

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CHAPTER I

WHAT ARE "SPECIES," AND WHAT IS MEANT BY THEIR "ORIGIN"

Definition of species--Special creation--The early

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before Darwin--The change of opinion effected by Darwin--The

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The title of Mr. Darwin's great work is--\_On the Origin of Species by

means of Natural Selection and the Preservation of Favoured Races in the

Struggle for Life\_. In order to appreciate fully the aim and object of

this work, and the change which it has effected not only in natural

history but in many other sciences, it is necessary to form a clear

conception of the meaning of the term "species," to know what was the

general belief regarding them at the time when Mr. Darwin's book first

appeared, and to understand what he meant, and what was generally meant,

by discovering their "origin." It is for want of this preliminary

knowledge that the majority of educated persons who are not naturalists

are so ready to accept the innumerable objections, criticisms, and

difficulties of its opponents as proofs that the Darwinian theory is

unsound, while it also renders them unable to appreciate, or even to

comprehend, the vast change which that theory has effected in the whole

mass of thought and opinion on the great question of evolution.

The term "species" was thus defined by the celebrated botanist De

Candolle: "A species is a collection of all the individuals which

resemble each other more than they resemble anything else, which can by

mutual fecundation produce fertile individuals, and which reproduce

themselves by generation, in such a manner that we may from analogy

suppose them all to have sprung from one single individual." And the

zoologist Swainson gives a somewhat similar definition: "A species, in

the usual acceptation of the term, is an animal which, in a state of

nature, is distinguished by certain peculiarities of form, size, colour,

or other circumstances, from another animal. It propagates, 'after its

kind,' individuals perfectly resembling the parent; its peculiarities,

therefore, are permanent."[1]

To illustrate these definitions we will take two common English birds,

the rook (Corvus frugilegus) and the crow (Corvus corone). These are

distinct \_species\_, because, in the first place, they always differ from

each other in certain slight peculiarities of structure, form, and

habits, and, in the second place, because rooks always produce rooks,

and crows produce crows, and they do not interbreed. It was therefore

concluded that all the rooks in the world had descended from a single

pair of rooks, and the crows in like manner from a single pair of crows,

while it was considered impossible that crows could have descended from

rooks or \_vice versÃ¢\_. The "origin" of the first pair of each kind was a

mystery. Similar remarks may be applied to our two common plants, the

sweet violet (Viola odorata) and the dog violet (Viola canina). These

also produce their like and never produce each other or intermingle, and

they were therefore each supposed to have sprung from a single

individual whose "origin" was unknown. But besides the crow and the rook

there are about thirty other kinds of birds in various parts of the

world, all so much like our species that they receive the common name of

crows; and some of them differ less from each other than does our crow

from our rook. These are all \_species\_ of the genus Corvus, and were

therefore believed to have been always as distinct as they are now,

neither more nor less, and to have each descended from one pair of

ancestral crows of the same identical species, which themselves had an

unknown "origin." Of violets there are more than a hundred different

kinds in various parts of the world, all differing very slightly from

each other and forming distinct \_species\_ of the genus Viola. But, as

these also each produce their like and do not intermingle, it was

believed that every one of them had always been as distinct from all the

others as it is now, that all the individuals of each kind had descended

from one ancestor, but that the "origin" of these hundred slightly

differing ancestors was unknown. In the words of Sir John Herschel,

quoted by Mr. Darwin, the origin of such species was "the mystery of

mysteries."

\_The Early Transmutationists\_.

A few great naturalists, struck by the very slight difference between

many of these species, and the numerous links that exist between the

most different forms of animals and plants, and also observing that a

great many species do vary considerably in their forms, colours, and

habits, conceived the idea that they might be all produced one from the

other. The most eminent of these writers was a great French naturalist,

Lamarck, who published an elaborate work, the \_Philosophie Zoologique\_,

in which he endeavoured to prove that all animals whatever are descended

from other species of animals. He attributed the change of species

chiefly to the effect of changes in the conditions of life--such as

climate, food, etc.--and especially to the desires and efforts of the

animals themselves to improve their condition, leading to a modification

of form or size in certain parts, owing to the well-known physiological

law that all organs are strengthened by constant use, while they are

weakened or even completely lost by disuse. The arguments of Lamarck did

not, however, satisfy naturalists, and though a few adopted the view

that closely allied species had descended from each other, the general

belief of the educated public was, that each species was a "special

creation" quite independent of all others; while the great body of

naturalists equally held, that the change from one species to another by

any known law or cause was impossible, and that the "origin of species"

was an unsolved and probably insoluble problem. The only other important

work dealing with the question was the celebrated \_Vestiges of

Creation\_, published anonymously, but now acknowledged to have been

written by the late Robert Chambers. In this work the action of general

laws was traced throughout the universe as a system of growth and

development, and it was argued that the various species of animals and

plants had been produced in orderly succession from each other by the

action of unknown laws of development aided by the action of external

conditions. Although this work had a considerable effect in influencing

public opinion as to the extreme improbability of the doctrine of the

independent "special creation" of each species, it had little effect

upon naturalists, because it made no attempt to grapple with the problem

in detail, or to show in any single case how the allied species of a

genus could have arisen, and have preserved their numerous slight and

apparently purposeless differences from each other. No clue whatever was

afforded to a law which should produce from any one species one or more

slightly differing but yet permanently distinct species, nor was any

reason given why such slight yet constant differences should exist at

all.

\_Scientific Opinion before Darwin.\_

In order to show how little effect these writers had upon the public

mind, I will quote a few passages from the writings of Sir Charles

Lyell, as representing the opinions of the most advanced thinkers in the

period immediately preceding that of Darwin's work. When recapitulating

the facts and arguments in favour of the invariability and permanence of

species, he says: "The entire variation from the original type which any

given kind of change can produce may usually be effected in a brief

period of time, after which no further deviation can be obtained by

continuing to alter the circumstances, though ever so gradually,

indefinite divergence either in the way of improvement or deterioration

being prevented, and the least possible excess beyond the defined limits

being fatal to the existence of the individual." In another place he

maintains that "varieties of some species may differ more than other

species do from each other without shaking our confidence in the reality

of species." He further adduces certain facts in geology as being, in

his opinion, "fatal to the theory of progressive development," and he

explains the fact that there are so often distinct species in countries

of similar climate and vegetation by "special creations" in each

country; and these conclusions were arrived at after a careful study of

Lamarck's work, a full abstract of which is given in the earlier

editions of the \_Principles of Geology\_.[2]

Professor Agassiz, one of the greatest naturalists of the last

generation, went even further, and maintained not only that each species

was specially created, but that it was created in the proportions and in

the localities in which we now find it to exist. The following extract

from his very instructive book on Lake Superior explains this view:

"There are in animals peculiar adaptations which are characteristic of

their species, and which cannot be supposed to have arisen from

subordinate influences. Those which live in shoals cannot be supposed to

have been created in single pairs. Those which are made to be the food

of others cannot have been created in the same proportions as those

which live upon them. Those which are everywhere found in innumerable

specimens must have been introduced in numbers capable of maintaining

their normal proportions to those which live isolated and are

comparatively and constantly fewer. For we know that this harmony in the

numerical proportions between animals is one of the great laws of

nature. The circumstance that species occur within definite limits where

no obstacles prevent their wider distribution leads to the further

inference that these limits were assigned to them from the beginning,

and so we should come to the final conclusion that the order which

prevails throughout nature is intentional, that it is regulated by the

limits marked out on the first day of creation, and that it has been

maintained unchanged through ages with no other modifications than those

which the higher intellectual powers of man enable him to impose on some

few animals more closely connected with him."[3]

These opinions of some of the most eminent and influential writers of

the pre-Darwinian age seem to us, now, either altogether obsolete or

positively absurd; but they nevertheless exhibit the mental condition of

even the most advanced section of scientific men on the problem of the

nature and origin of species. They render it clear that,

notwithstanding the vast knowledge and ingenious reasoning of Lamarck,

and the more general exposition of the subject by the author of the

\_Vestiges of Creation\_, the first step had not been taken towards a

satisfactory explanation of the derivation of any one species from any

other. Such eminent naturalists as Geoffroy Saint Hilaire, Dean Herbert,

Professor Grant, Von Buch, and some others, had expressed their belief

that species arose as simple varieties, and that the species of each

genus were all descended from a common ancestor; but none of them gave a

clue as to the law or the method by which the change had been effected.

This was still "the great mystery." As to the further question--how far

this common descent could be carried; whether distinct families, such as

crows and thrushes, could possibly have descended from each other; or,

whether all birds, including such widely distinct types as wrens,

eagles, ostriches, and ducks, could all be the modified descendants of a

common ancestor; or, still further, whether mammalia, birds, reptiles,

and fishes, could all have had a common origin;--these questions had

hardly come up for discussion at all, for it was felt that, while the

very first step along the road of "transmutation of species" (as it was

then called) had not been made, it was quite useless to speculate as to

how far it might be possible to travel in the same direction, or where

the road would ultimately lead to.

\_The Problem before Darwin\_.

It is clear, then, that what was understood by the "origin" or the

"transmutation" of species before Darwin's work appeared, was the

comparatively simple question whether the allied species of each genus

had or had not been derived from one another and, remotely, from some

common ancestor, by the ordinary method of reproduction and by means of

laws and conditions still in action and capable of being thoroughly

investigated. If any naturalist had been asked at that day whether,

supposing it to be clearly shown that all the different species of each

genus had been derived from some one ancestral species, and that a full

and complete explanation were to be given of how each minute difference

in form, colour, or structure might have originated, and how the

several peculiarities of habit and of geographical distribution might

have been brought about--whether, if this were done, the "origin of

species" would be discovered, the great mystery solved, he would

undoubtedly have replied in the affirmative. He would probably have

added that he never expected any such marvellous discovery to be made in

his lifetime. But so much as this assuredly Mr. Darwin has done, not

only in the opinion of his disciples and admirers, but by the admissions

of those who doubt the completeness of his explanations. For almost all

their objections and difficulties apply to those larger differences

which separate genera, families, and orders from each other, not to

those which separate one species from the species to which it is most

nearly allied, and from the remaining species of the same genus. They

adduce such difficulties as the first development of the eye, or of the

milk-producing glands of the mammalia; the wonderful instincts of bees

and of ants; the complex arrangements for the fertilisation of orchids,

and numerous other points of structure or habit, as not being

satisfactorily explained. But it is evident that these peculiarities had

their origin at a very remote period of the earth's history, and no

theory, however complete, can do more than afford a probable conjecture

as to how they were produced. Our ignorance of the state of the earth's

surface and of the conditions of life at those remote periods is very

great; thousands of animals and plants must have existed of which we

have no record; while we are usually without any information as to the

habits and general life-history even of those of which we possess some

fragmentary remains; so that the truest and most complete theory would

not enable us to solve \_all\_ the difficult problems which the whole

course of the development of life upon our globe presents to us.

What we may expect a true theory to do is to enable us to comprehend and

follow out in some detail those changes in the form, structure, and

relations of animals and plants which are effected in short periods of

time, geologically speaking, and which are now going on around us. We

may expect it to explain satisfactorily most of the lesser and

superficial differences which distinguish one species from another. We

may expect it to throw light on the mutual relations of the animals and

plants which live together in any one country, and to give some rational

account of the phenomena presented by their distribution in different

parts of the world. And, lastly, we may expect it to explain many

difficulties and to harmonise many incongruities in the excessively

complex affinities and relations of living things. All this the

Darwinian theory undoubtedly does. It shows us how, by means of some of

the most universal and ever-acting laws in nature, new species are

necessarily produced, while the old species become extinct; and it

enables us to understand how the continuous action of these laws during

the long periods with which geology makes us acquainted is calculated to

bring about those greater differences presented by the distinct genera,

families, and orders into which all living things are classified by

naturalists. The differences which these present are all of the same

\_nature\_ as those presented by the species of many large genera, but

much greater in \_amount\_; and they can all be explained by the action of

the same general laws and by the extinction of a larger or smaller

number of intermediate species. Whether the distinctions between the

higher groups termed Classes and Sub-kingdoms may be accounted for in

the same way is a much more difficult question. The differences which

separate the mammals, birds, reptiles, and fishes from each other,

though vast, yet seem of the same nature as those which distinguish a

mouse from an elephant or a swallow from a goose. But the vertebrate

animals, the mollusca, and the insects, are so radically distinct in

their whole organisation and in the very plan of their structure, that

objectors may not unreasonably doubt whether they can all have been

derived from a common ancestor by means of the very same laws as have

sufficed for the differentiation of the various species of birds or of

reptiles.

\_The Change of Opinion effected by Darwin\_.

The point I wish especially to urge is this. Before Darwin's work

appeared, the great majority of naturalists, and almost without

exception the whole literary and scientific world, held firmly to the

belief that \_species\_ were realities, and had not been derived from

other species by any process accessible to us; the different species of

crow and of violet they are now, and to have originated by some totally

unknown process so far removed from ordinary reproduction that it was

usually spoken of as "special creation." There was, then, no question of

the origin of families, orders, and classes, because the very first step

of all, the "origin of species," was believed to be an insoluble

problem. But now this is all changed. The whole scientific and literary

world, even the whole educated public, accepts, as a matter of common

knowledge, the origin of species from other allied species by the

ordinary process of natural birth. The idea of special creation or any

altogether exceptional mode of production is absolutely extinct! Yet

more: this is held also to apply to many higher groups as well as to the

species of a genus, and not even Mr. Darwin's severest critics venture

to suggest that the primeval bird, reptile, or fish must have been

"specially created." And this vast, this totally unprecedented change in

public opinion has been the result of the work of one man, and was

brought about in the short space of twenty years! This is the answer to

those who continue to maintain that the "origin of species" is not yet

discovered; that there are still doubts and difficulties; that there are

divergencies of structure so great that we cannot understand how they

had their beginning. We may admit all this, just as we may admit that

there are enormous difficulties in the way of a complete comprehension

of the origin and nature of all the parts of the solar system and of the

stellar universe. But we claim for Darwin that he is the Newton of

natural history, and that, just so surely as that the discovery and

demonstration by Newton of the law of gravitation established order in

place of chaos and laid a sure foundation for all future study of the

starry heavens, so surely has Darwin, by his discovery of the law of

natural selection and his demonstration of the great principle of the

preservation of useful variations in the struggle for life, not only

thrown a flood of light on the process of development of the whole

organic world, but also established a firm foundation for all future

study of nature.

In order to show the view Darwin took of his own work, and what it was

that he alone claimed to have done, the concluding passage of the

introduction to the \_Origin of\_ \_Species\_ should be carefully

considered. It is as follows: "Although much remains obscure, and will

long remain obscure, I can entertain no doubt, after the most deliberate

and dispassionate judgment of which I am capable, that the view which

most naturalists until recently entertained and which I formerly

entertained--namely, that each species has been independently

created--is erroneous. I am fully convinced that species are not

immutable; but that those belonging to what are called the same genera

are lineal descendants of some other and generally extinct species, in

the same manner as the acknowledged varieties of any one species are the

descendants of that species. Furthermore, I am convinced that Natural

Selection has been the most important, but not the exclusive, means of

modification."

It should be especially noted that all which is here claimed is now

almost universally admitted, while the criticisms of Darwin's works

refer almost exclusively to those numerous questions which, as he

himself says, "will long remain obscure."

\_The Darwinian Theory\_.

As it will be necessary, in the following chapters, to set forth a

considerable body of facts in almost every department of natural

history, in order to establish the fundamental propositions on which the

theory of natural selection rests, I propose to give a preliminary

statement of what the theory really is, in order that the reader may

better appreciate the necessity for discussing so many details, and may

thus feel a more enlightened interest in them. Many of the facts to be

adduced are so novel and so curious that they are sure to be appreciated

by every one who takes an interest in nature, but unless the need of

them is clearly seen it may be thought that time is being wasted on mere

curious details and strange facts which have little bearing on the

question at issue.

The theory of natural selection rests on two main classes of facts which

apply to all organised beings without exception, and which thus take

rank as fundamental principles or laws. The first is, the power of rapid

multiplication in a geometrical progression; the second, that the

offspring always vary slightly from the parents, though generally very

closely resembling them. From the first fact or law there follows,

necessarily, a constant struggle for existence; because, while the

offspring always exceed the parents in number, generally to an enormous

extent, yet the total number of living organisms in the world does not,

and cannot, increase year by year. Consequently every year, on the

average, as many die as are born, plants as well as animals; and the

majority die premature deaths. They kill each other in a thousand

different ways; they starve each other by some consuming the food that

others want; they are destroyed largely by the powers of nature--by cold

and heat, by rain and storm, by flood and fire. There is thus a

perpetual struggle among them which shall live and which shall die; and

this struggle is tremendously severe, because so few can possibly remain

alive--one in five, one in ten, often only one in a hundred or even one

in a thousand.

Then comes the question, Why do some live rather than others? If all the

individuals of each species were exactly alike in every respect, we

could only say it is a matter of chance. But they are not alike. We find

that they vary in many different ways. Some are stronger, some swifter,

some hardier in constitution, some more cunning. An obscure colour may

render concealment more easy for some, keener sight may enable others to

discover prey or escape from an enemy better than their fellows. Among

plants the smallest differences may be useful or the reverse. The

earliest and strongest shoots may escape the slug; their greater vigour

may enable them to flower and seed earlier in a wet autumn; plants best

armed with spines or hairs may escape being devoured; those whose

flowers are most conspicuous may be soonest fertilised by insects. We

cannot doubt that, on the whole, any beneficial variations will give the

possessors of it a greater probability of living through the tremendous

ordeal they have to undergo. There may be something left to chance, but

on the whole \_the fittest will survive\_.

Then we have another important fact to consider, the principle of

heredity or transmission of variations. If we grow plants from seed or

breed any kind of animals year after year, consuming or giving away all

the increase we do not wish to keep just as they come to hand, our

plants or animals will continue much the same; but if every year we

carefully save the best seed to sow and the finest or brightest

coloured animals to breed from, we shall soon find that an improvement

will take place, and that the average quality of our stock will be

raised. This is the way in which all our fine garden fruits and

vegetables and flowers have been produced, as well as all our splendid

breeds of domestic animals; and they have thus become in many cases so

different from the wild races from which they originally sprang as to be

hardly recognisable as the same. It is therefore proved that if any

particular kind of variation is preserved and bred from, the variation

itself goes on increasing in amount to an enormous extent; and the

bearing of this on the question of the origin of species is most

important. For if in each generation of a given animal or plant the

fittest survive to continue the breed, then whatever may be the special

peculiarity that causes "fitness" in the particular case, that

peculiarity will go on increasing and strengthening \_so long as it is

useful to the species\_. But the moment it has reached its maximum of

usefulness, and some other quality or modification would help in the

struggle, then the individuals which vary in the new direction will

survive; and thus a species may be gradually modified, first in one

direction, then in another, till it differs from the original parent

form as much as the greyhound differs from any wild dog or the

cauliflower from any wild plant. But animals or plants which thus differ

in a state of nature are always classed as distinct species, and thus we

see how, by the continuous survival of the fittest or the preservation

of favoured races in the struggle for life, new species may be

originated.

This self-acting process which, by means of a few easily demonstrated

groups of facts, brings about change in the organic world, and keeps

each species in harmony with the conditions of its existence, will

appear to some persons so clear and simple as to need no further

demonstration. But to the great majority of naturalists and men of

science endless difficulties and objections arise, owing to the

wonderful variety of animal and vegetable forms, and the intricate

relations of the different species and groups of species with each

other; and it was to answer as many of these objections as possible, and

to show that the more we know of nature the more we find it to

harmonise with the development hypothesis, that Darwin devoted the whole

of his life to collecting facts and making experiments, the record of a

portion of which he has given us in a series of twelve masterly volumes.

\_Proposed Mode of Treatment of the Subject\_.

It is evidently of the most vital importance to any theory that its

foundations should be absolutely secure. It is therefore necessary to

show, by a wide and comprehensive array of facts, that animals and

plants \_do\_ perpetually vary in the manner and to the amount requisite;

and that this takes place in wild animals as well as in those which are

domesticated. It is necessary also to prove that all organisms \_do\_ tend

to increase at the great rate alleged, and that this increase actually

occurs, under favourable conditions. We have to prove, further, that

variations of all kinds can be increased and accumulated by selection;

and that the struggle for existence to the extent here indicated

actually occurs in nature, and leads to the continued preservation of

favourable variations.

These matters will be discussed in the four succeeding chapters, though

in a somewhat different order--the struggle for existence and the power

of rapid multiplication, which is its cause, occupying the first place,

as comprising those facts which are the most fundamental and those which

can be perfectly explained without any reference to the less generally

understood facts of variation. These chapters will be followed by a

discussion of certain difficulties, and of the vexed question of

hybridity. Then will come a rather full account of the more important of

the complex relations of organisms to each other and to the earth

itself, which are either fully explained or greatly elucidated by the

theory. The concluding chapter will treat of the origin of man and his

relations to the lower animals.

FOOTNOTES:

[Footnote 1: \_Geography and Classification of Animals\_, p. 350.]

[Footnote 2: These expressions occur in Chapter IX. of the earlier

editions (to the ninth) of the \_Principles of Geology\_.]

[Footnote 3: L. Agassiz, \_Lake Superior\_, p. 377.]

CHAPTER II

THE STRUGGLE FOR EXISTENCE

Its importance--The struggle among plants--Among

animals--Illustrative cases--Succession of trees in forests of

Denmark--The struggle for existence on the Pampas--Increase of

organisms in a geometrical ratio--Examples of great powers of

increase of animals--Rapid increase and wide spread of

plants--Great fertility not essential to rapid

increase--Struggle between closely allied species most

severe--The ethical aspect of the struggle for existence.

There is perhaps no phenomenon of nature that is at once so important,

so universal; and so little understood, as the struggle for existence

continually going on among all organised beings. To most persons nature

appears calm, orderly, and peaceful. They see the birds singing in the

trees, the insects hovering over the flowers, the squirrel climbing

among the tree-tops, and all living things in the possession of health

and vigour, and in the enjoyment of a sunny existence. But they do not

see, and hardly ever think of, the means by which this beauty and

harmony and enjoyment is brought about. They do not see the constant and

daily search after food, the failure to obtain which means weakness or

death; the constant effort to escape enemies; the ever-recurring

struggle against the forces of nature. This daily and hourly struggle,

this incessant warfare, is nevertheless the very means by which much of

the beauty and harmony and enjoyment in nature is produced, and also

affords one of the most important elements in bringing about the origin

of species. We must, therefore, devote some time to the consideration of

its various aspects and of the many curious phenomena to which it gives

rise.

It is a matter of common observation that if weeds are allowed to grow

unchecked in a garden they will soon destroy a number of the flowers.

It is not so commonly known that if a garden is left to become

altogether wild, the weeds that first take possession of it, often

covering the whole surface of the ground with two or three different

kinds, will themselves be supplanted by others, so that in a few years

many of the original flowers and of the earliest weeds may alike have

disappeared. This is one of the very simplest cases of the struggle for

existence, resulting in the successive displacement of one set of

species by another; but the exact causes of this displacement are by no

means of such a simple nature. All the plants concerned may be perfectly

hardy, all may grow freely from seed, yet when left alone for a number

of years, each set is in turn driven out by a succeeding set, till at

the end of a considerable period--a century or a few centuries

perhaps--hardly one of the plants which first monopolised the ground

would be found there.

Another phenomenon of an analogous kind is presented by the different

behaviour of introduced wild plants or animals into countries apparently

quite as well suited to them as those which they naturally inhabit.

Agassiz, in his work on Lake Superior, states that the roadside weeds of

the northeastern United States, to the number of 130 species, are all

European, the native weeds having disappeared westwards; and in New

Zealand there are no less than 250 species of naturalised European

plants, more than 100 species of which have spread widely over the

country, often displacing the native vegetation. On the other hand, of

the many hundreds of hardy plants which produce seed freely in our

gardens, very few ever run wild, and hardly any have become common. Even

attempts to naturalise suitable plants usually fail; for A. de Candolle

states that several botanists of Paris, Geneva, and especially of

Montpellier, have sown the seeds of many hundreds of species of hardy

exotic plants in what appeared to be the most favourable situations, but

that, in hardly a single case, has any one of them become

naturalised.[4] Even a plant like the potato--so widely cultivated, so

hardy, and so well adapted to spread by means of its many-eyed

tubers--has not established itself in a wild state in any part of

Europe. It would be thought that Australian plants would easily run

wild in New Zealand. But Sir Joseph Hooker informs us that the late Mr.

Bidwell habitually scattered Australian seeds during his extensive

travels in New Zealand, yet only two or three Australian plants appear

to have established themselves in that country, and these only in

cultivated or newly moved soil.

These few illustrations sufficiently show that all the plants of a

country are, as De Candolle says, at war with each other, each one

struggling to occupy ground at the expense of its neighbour. But,

besides this direct competition, there is one not less powerful arising

from the exposure of almost all plants to destruction by animals. The

buds are destroyed by birds, the leaves by caterpillars, the seeds by

weevils; some insects bore into the trunk, others burrow in the twigs

and leaves; slugs devour the young seedlings and the tender shoots,

wire-worms gnaw the roots. Herbivorous mammals devour many species

bodily, while some uproot and devour the buried tubers.

In animals, it is the eggs or the very young that suffer most from their

various enemies; in plants, the tender seedlings when they first appear

above the ground. To illustrate this latter point Mr. Darwin cleared and

dug a piece of ground three feet long and two feet wide, and then marked

all the seedlings of weeds and other plants which came up, noting what

became of them. The total number was 357, and out of these no less than

295 were destroyed by slugs and insects. The direct strife of plant with

plant is almost equally fatal when the stronger are allowed to smother

the weaker. When turf is mown or closely browsed by animals, a number of

strong and weak plants live together, because none are allowed to grow

much beyond the rest; but Mr. Darwin found that when the plants which

compose such turf are allowed to grow up freely, the stronger kill the

weaker. In a plot of turf three feet by four, twenty distinct species of

plants were found to be growing, and no less than nine of these perished

altogether when the other species were allowed to grow up to their full

size.[5]

But besides having to protect themselves against competing plants and

against destructive animals, there is a yet deadlier enemy in the

forces of inorganic nature. Each species can sustain a certain amount of

heat and cold, each requires a certain amount of moisture at the right

season, each wants a proper amount of light or of direct sunshine, each

needs certain elements in the soil; the failure of a due proportion in

these inorganic conditions causes weakness, and thus leads to speedy

death. The struggle for existence in plants is, therefore, threefold in

character and infinite in complexity, and the result is seen in their

curiously irregular distribution over the face of the earth. Not only

has each country its distinct plants, but every valley, every hillside,

almost every hedgerow, has a different set of plants from its adjacent

valley, hillside, or hedgerow--if not always different in the actual

species yet very different in comparative abundance, some which are rare

in the one being common in the other. Hence it happens that slight

changes of conditions often produce great changes in the flora of a

country. Thus in 1740 and the two following years the larva of a moth

(Phalaena graminis) committed such destruction in many of the meadows of

Sweden that the grass was greatly diminished in quantity, and many

plants which were before choked by the grass sprang up, and the ground

became variegated with a multitude of different species of flowers. The

introduction of goats into the island of St. Helena led to the entire

destruction of the native forests, consisting of about a hundred

distinct species of trees and shrubs, the young plants being devoured by

the goats as fast as they grew up. The camel is a still greater enemy to

woody vegetation than the goat, and Mr. Marsh believes that forests

would soon cover considerable tracts of the Arabian and African deserts

if the goat and the camel were removed from them.[6] Even in many parts

of our own country the existence of trees is dependent on the absence of

cattle. Mr. Darwin observed, on some extensive heaths near Farnham, in

Surrey, a few clumps of old Scotch firs, but no young trees over

hundreds of acres. Some portions of the heath had, however, been

enclosed a few years before, and these enclosures were crowded with

young fir-trees growing too close together for all to live; and these

were not sown or planted, nothing having been done to the ground beyond

enclosing it so as to keep out cattle. On ascertaining this, Mr. Darwin

was so much surprised that he searched among the heather in the

unenclosed parts, and there he found multitudes of little trees and

seedlings which had been perpetually browsed down by the cattle. In one

square yard, at a point about a hundred yards from one of the old clumps

of firs, he counted thirty-two little trees, and one of them had

twenty-six rings of growth, showing that it had for many years tried to

raise its head above the stems of the heather and had failed. Yet this

heath was very extensive and very barren, and, as Mr. Darwin remarks, no

one would ever have imagined that cattle would have so closely and so

effectually searched it for food.

In the case of animals, the competition and struggle are more obvious.

The vegetation of a given district can only support a certain number of

animals, and the different kinds of plant-eaters will compete together

for it. They will also have insects for their competitors, and these

insects will be kept down by birds, which will thus assist the mammalia.

But there will also be carnivora destroying the herbivora; while small

rodents, like the lemming and some of the field-mice, often destroy so

much vegetation as materially to affect the food of all the other groups

of animals. Droughts, floods, severe winters, storms and hurricanes will

injure these in various degrees, but no one species can be diminished in

numbers without the effect being felt in various complex ways by all the

rest. A few illustrations of this reciprocal action must be given.

\_Illustrative Cases of the Struggle for Life\_.

Sir Charles Lyell observes that if, by the attacks of seals or other

marine foes, salmon are reduced in numbers, the consequence will be that

otters, living far inland, will be deprived of food and will then

destroy many young birds or quadrupeds, so that the increase of a marine

animal may cause the destruction of many land animals hundreds of miles

away. Mr. Darwin carefully observed the effects produced by planting a

few hundred acres of Scotch fir, in Staffordshire, on part of a very

extensive heath which had never been cultivated. After the planted

portion was about twenty-five years old he observed that the change in

the native vegetation was greater than is often seen in passing from

one quite different soil to another. Besides a great change in the

proportional numbers of the native heath-plants, twelve species which

could not be found on the heath flourished in the plantations. The

effect on the insect life must have been still greater, for six

insectivorous birds which were very common in the plantations were not

to be seen on the heath, which was, however, frequented by two or three

different species of insectivorous birds. It would have required

continued study for several years to determine all the differences in

the organic life of the two areas, but the facts stated by Mr. Darwin

are sufficient to show how great a change may be effected by the

introduction of a single kind of tree and the keeping out of cattle.

The next case I will give in Mr. Darwin's own words: "In several parts

of the world insects determine the existence of cattle. Perhaps Paraguay

offers the most curious instance of this; for here neither cattle nor

horses nor dogs have ever run wild, though they swarm southward and

northward in a feral state; and Azara and Rengger have shown that this

is caused by the greater numbers, in Paraguay, of a certain fly which

lays its eggs in the navels of these animals when first born. The

increase of these flies, numerous as they are, must be habitually

checked by some means, probably by other parasitic insects. Hence, if

certain insectivorous birds were to decrease in Paraguay, the parasitic

insects would probably increase; and this would lessen the number of the

navel-frequenting flies--then cattle and horses would become feral, and

this would greatly alter (as indeed I have observed in parts of South

America) the vegetation: this again would largely affect the insects,

and this, as we have just seen in Staffordshire, the insectivorous

birds, and so onward in ever-increasing circles of complexity. Not that

under nature the relations will ever be as simple as this. Battle within

battle must be continually recurring with varying success; and yet in

the long run the forces are so nicely balanced, that the face of nature

remains for a long time uniform, though assuredly the merest trifle

would give the victory to one organic being over another."[7]

Such cases as the above may perhaps be thought exceptional, but there

is good reason to believe that they are by no means rare, but are

illustrations of what is going on in every part of the world, only it is

very difficult for us to trace out the complex reactions that are

everywhere occurring. The general impression of the ordinary observer

seems to be that wild animals and plants live peaceful lives and have

few troubles, each being exactly suited to its place and surroundings,

and therefore having no difficulty in maintaining itself. Before showing

that this view is, everywhere and always, demonstrably untrue, we will

consider one other case of the complex relations of distinct organisms

adduced by Mr. Darwin, and often quoted for its striking and almost

eccentric character. It is now well known that many flowers require to

be fertilised by insects in order to produce seed, and this

fertilisation can, in some cases, only be effected by one particular

species of insect to which the flower has become specially adapted. Two

of our common plants, the wild heart's-ease (Viola tricolor) and the red

clover (Trifolium pratense), are thus fertilised by humble-bees almost

exclusively, and if these insects are prevented from visiting the

flowers, they produce either no seed at all or exceedingly few. Now it

is known that field-mice destroy the combs and nests of humble-bees, and

Colonel Newman, who has paid great attention to these insects, believes

that more than two-thirds of all the humble-bees' nests in England are

thus destroyed. But the number of mice depends a good deal on the number

of cats; and the same observer says that near villages and towns he has

found the nests of humble-bees more numerous than elsewhere, which he

attributes to the number of cats that destroy the mice. Hence it

follows, that the abundance of red clover and wild heart's-ease in a

district will depend on a good supply of cats to kill the mice, which

would otherwise destroy and keep down the humble-bees and prevent them

from fertilising the flowers. A chain of connection has thus been found

between such totally distinct organisms as flesh-eating mammalia and

sweet-smelling flowers, the abundance or scarcity of the one closely

corresponding to that of the other!

The following account of the struggle between trees in the forests of

Denmark, from the researches of M. Hansten-Blangsted, strikingly

illustrates our subject.[8] The chief combatants are the beech and the

birch, the former being everywhere successful in its invasions. Forests

composed wholly of birch are now only found in sterile, sandy tracts;

everywhere else the trees are mixed, and wherever the soil is favourable

the beech rapidly drives out the birch. The latter loses its branches at

the touch of the beech, and devotes all its strength to the upper part

where it towers above the beech. It may live long in this way, but it

succumbs ultimately in the fight--of old age if of nothing else, for the

life of the birch in Denmark is shorter than that of the beech. The

writer believes that light (or rather shade) is the cause of the

superiority of the latter, for it has a greater development of its

branches than the birch, which is more open and thus allows the rays of

the sun to pass through to the soil below, while the tufted, bushy top

of the beech preserves a deep shade at its base. Hardly any young plants

can grow under the beech except its own shoots; and while the beech can

nourish under the shade of the birch, the latter dies immediately under

the beech. The birch has only been saved from total extermination by the

facts that it had possession of the Danish forests long before the beech

ever reached the country, and that certain districts are unfavourable to

the growth of the latter. But wherever the soil has been enriched by the

decomposition of the leaves of the birch the battle begins. The birch

still flourishes on the borders of lakes and other marshy places, where

its enemy cannot exist. In the same way, in the forests of Zeeland, the

fir forests are disappearing before the beech. Left to themselves, the

firs are soon displaced by the beech. The struggle between the latter

and the oak is longer and more stubborn, for the branches and foliage of

the oak are thicker, and offer much resistance to the passage of light.

The oak, also, has greater longevity; but, sooner or later, it too

succumbs, because it cannot develop in the shadow of the beech. The

earliest forests of Denmark were mainly composed of aspens, with which

the birch was apparently associated; gradually the soil was raised, and

the climate grew milder; then the fir came and formed large forests.

This tree ruled for centuries, and then ceded the first place to the

holm-oak, which is now giving way to the beech. Aspen, birch, fir, oak,

and beech appear to be the steps in the struggle for the survival of the

fittest among the forest-trees of Denmark.

It may be added that in the time of the Romans the beech was the

principal forest-tree of Denmark as it is now, while in the much earlier

bronze age, represented by the later remains found in the peat bogs,

there were no beech-trees, or very few, the oak being the prevailing

tree, while in the still earlier stone period the fir was the most

abundant. The beech is a tree essentially of the temperate zone, having

its northern limit considerably southward of the oak, fir, birch, or

aspen, and its entrance into Denmark was no doubt due to the

amelioration of the climate after the glacial epoch had entirely passed

away. We thus see how changes of climate, which are continually

occurring owing either to cosmical or geographical causes, may initiate

a struggle among plants which may continue for thousands of years, and

which must profoundly modify the relations of the animal world, since

the very existence of innumerable insects, and even of many birds and

mammals, is dependent more or less completely on certain species of

plants.

\_The Struggle for Existence on the Pampas\_.

Another illustration of the struggle for existence, in which both plants

and animals are implicated, is afforded by the pampas of the southern

part of South America. The absence of trees from these vast plains has

been imputed by Mr. Darwin to the supposed inability of the tropical and

sub-tropical forms of South America to thrive on them, and there being

no other source from which they could obtain a supply; and that

explanation was adopted by such eminent botanists as Mr. Ball and

Professor Asa Gray. This explanation has always seemed to me

unsatisfactory, because there are ample forests both in the temperate

regions of the Andes and on the whole west coast down to Terra del

Fuego; and it is inconsistent with what we know of the rapid variation

and adaptation of species to new conditions. What seems a more

satisfactory explanation has been given by Mr. Edwin Clark, a civil

engineer, who resided nearly two years in the country and paid much

attention to its natural history. He says: "The peculiar characteristics

of these vast level plains which descend from the Andes to the great

river basin in unbroken monotony, are the absence of rivers or

water-storage, and the periodical occurrence of droughts, or 'siccos,'

in the summer months. These conditions determine the singular character

both of its flora and fauna.

"The soil is naturally fertile and favourable for the growth of trees,

and they grow luxuriantly wherever they are protected. The eucalyptus is

covering large tracts wherever it is enclosed, and willows, poplars, and

the fig surround every estancia when fenced in.

"The open plains are covered with droves of horses and cattle, and

overrun by numberless wild rodents, the original tenants of the pampas.

During the long periods of drought, which are so great a scourge to the

country, these animals are starved by thousands, destroying, in their

efforts to live, every vestige of vegetation. In one of these 'siccos,'

at the time of my visit, no less than 50,000 head of oxen and sheep and

horses perished from starvation and thirst, after tearing deep out of

the soil every trace of vegetation, including the wiry roots of the

pampas-grass. Under such circumstances the existence of an unprotected

tree is impossible. The only plants that hold their own, in addition to

the indestructible thistles, grasses, and clover, are a little

herbaceous oxalis, producing viviparous buds of extraordinary vitality,

a few poisonous species, such as the hemlock, and a few tough, thorny

dwarf-acacias and wiry rushes, which even a starving rat refuses.

"Although the cattle are a modern introduction, the numberless

indigenous rodents must always have effectually prevented the

introduction of any other species of plants; large tracts are still

honeycombed by the ubiquitous biscacho, a gigantic rabbit; and numerous

other rodents still exist, including rats and mice, pampas-hares, and

the great nutria and carpincho (capybara) on the river banks."[9]

Mr. Clark further remarks on the desperate struggle for existence which

characterises the bordering fertile zones, where rivers and marshy

plains permit a more luxuriant and varied vegetable and animal life.

After describing how the river sometimes rose 30 feet in eight hours,

doing immense destruction, and the abundance of the larger carnivora and

large reptiles on its banks, he goes on: "But it was among the flora

that the principle of natural selection was most prominently displayed.

In such a district--overrun with rodents and escaped cattle, subject to

floods that carried away whole islands of botany, and especially to

droughts that dried up the lakes and almost the river itself--no

ordinary plant could live, even on this rich and watered alluvial

debris. The only plants that escaped the cattle were such as were either

poisonous, or thorny, or resinous, or indestructibly tough. Hence we had

only a great development of solanums, talas, acacias, euphorbias, and

laurels. The buttercup is replaced by the little poisonous yellow oxalis

with its viviparous buds; the passion-flowers, asclepiads, bignonias,

convolvuluses, and climbing leguminous plants escape both floods and

cattle by climbing the highest trees and towering overhead in a flood of

bloom. The ground plants are the portulacas, turneras, and cenotheras,

bitter and ephemeral, on the bare rock, and almost independent of any

other moisture than the heavy dews. The pontederias, alismas, and

plantago, with grasses and sedges, derive protection from the deep and

brilliant pools; and though at first sight the 'monte' doubtless

impresses the traveller as a scene of the wildest confusion and ruin,

yet, on closer examination, we found it far more remarkable as a

manifestation of harmony and law, and a striking example of the

marvellous power which plants, like animals, possess, of adapting

themselves to the local peculiarities of their habitat, whether in the

fertile shades of the luxuriant 'monte' or on the arid, parched-up

plains of the treeless pampas."

A curious example of the struggle between plants has been communicated

to me by Mr. John Ennis, a resident in New Zealand. The English

water-cress grows so luxuriantly in that country as to completely choke

up the rivers, sometimes leading to disastrous floods, and necessitating

great outlay to keep the stream open. But a natural remedy has now been

found in planting willows on the banks. The roots of these trees

penetrate the bed of the stream in every direction, and the water-cress,

unable to obtain the requisite amount of nourishment, gradually

disappears.

\_Increase of Organisms in a Geometrical Ratio\_.

The facts which have now been adduced, sufficiently prove that there is

a continual competition, and struggle, and war going on in nature, and

that each species of animal and plant affects many others in complex and

often unexpected ways. We will now proceed to show the fundamental cause

of this struggle, and to prove that it is ever acting over the whole

field of nature, and that no single species of animal or plant can

possibly escape from it. This results from the fact of the rapid

increase, in a geometrical ratio, of all the species of animals and

plants. In the lower orders this increase is especially rapid, a single

flesh-fly (Musca carnaria) producing 20,000 larvae, and these growing so

quickly that they reach their full size in five days; hence the great

Swedish naturalist, Linnaeus, asserted that a dead horse would be

devoured by three of these flies as quickly as by a lion. Each of these

larvae remains in the pupa state about five or six days, so that each

parent fly may be increased ten thousand-fold in a fortnight. Supposing

they went on increasing at this rate during only three months of summer,

there would result one hundred millions of millions of millions for each

fly at the commencement of summer,--a number greater probably than

exists at any one time in the whole world. And this is only one species,

while there are thousands of other species increasing also at an

enormous rate; so that, if they were unchecked, the whole atmosphere

would be dense with flies, and all animal food and much of animal life

would be destroyed by them. To prevent this tremendous increase there

must be incessant war against these insects, by insectivorous birds and

reptiles as well as by other insects, in the larva as well as in the

perfect state, by the action of the elements in the form of rain, hail,

or drought, and by other unknown causes; yet we see nothing of this

ever-present war, though by its means alone, perhaps, we are saved from

famine and pestilence.

Let us now consider a less extreme and more familiar case. We possess a

considerable number of birds which, like the redbreast, sparrow, the

four common titmice, the thrush, and the blackbird, stay with us all the

year round These lay on an average six eggs, but, as several of them

have two or more broods a year, ten will be below the average of the

year's increase. Such birds as these often live from fifteen to twenty

years in confinement, and we cannot suppose them to live shorter lives

in a state of nature, if unmolested; but to avoid possible exaggeration

we will take only ten years as the average duration of their lives. Now,

if we start with a single pair, and these are allowed to live and breed,

unmolested, till they die at the end of ten years,--as they might do if

turned loose into a good-sized island with ample vegetable and insect

food, but no other competing or destructive birds or quadrupeds--their

numbers would amount to more than twenty millions. But we know very well

that our bird population is no greater, on the average, now than it was

ten years ago. Year by year it may fluctuate a little according as the

winters are more or less severe, or from other causes, but on the whole

there is no increase. What, then, becomes of the enormous surplus

population annually produced? It is evident they must all die or be

killed, somehow; and as the increase is, on the average, about five to

one, it follows that, if the average number of birds of all kinds in our

islands is taken at ten millions--and this is probably far under the

mark--then about fifty millions of birds, including eggs as possible

birds, must annually die or be destroyed. Yet we see nothing, or almost

nothing, of this tremendous slaughter of the innocents going on all

around us. In severe winters a few birds are found dead, and a few

feathers or mangled remains show us where a wood-pigeon or some other

bird has been destroyed by a hawk, but no one would imagine that five

times as many birds as the total number in the country in early spring

die every year. No doubt a considerable proportion of these do not die

here but during or after migration to other countries, but others which

are bred in distant countries come here, and thus balance the account.

Again, as the average number of young produced is four or five times

that of the parents, we ought to have at least five times as many birds

in the country at the end of summer as at the beginning, and there is

certainly no such enormous disproportion as this. The fact is, that the

destruction commences, and is probably most severe, with nestling birds,

which are often killed by heavy rains or blown away by severe storms, or

left to die of hunger if either of the parents is killed; while they

offer a defenceless prey to jackdaws, jays, and magpies, and not a few

are ejected from their nests by their foster-brothers the cuckoos. As

soon as they are fledged and begin to leave the nest great numbers are

destroyed by buzzards, sparrow-hawks, and shrikes. Of those which

migrate in autumn a considerable proportion are probably lost at sea or

otherwise destroyed before they reach a place of safety; while those

which remain with us are greatly thinned by cold and starvation during

severe winters. Exactly the same thing goes on with every species of

wild animal and plant from the lowest to the highest. All breed at such

a rate, that in a few years the progeny of any one species would, if

allowed to increase unchecked, alone monopolise the land; but all alike

are kept within bounds by various destructive agencies, so that, though

the numbers of each may fluctuate, they can never permanently increase

except at the expense of some others, which must proportionately

decrease.

\_Cases showing the Great Powers of Increase of Animals.\_

As the facts now stated are the very foundation of the theory we are

considering, and the enormous increase and perpetual destruction

continually going on require to be kept ever present in the mind, some

direct evidence of actual cases of increase must be adduced. That even

the larger animals, which breed comparatively slowly, increase

enormously when placed under favourable conditions in new countries, is

shown by the rapid spread of cattle and horses in America. Columbus, in

his second voyage, left a few black cattle at St. Domingo, and these ran

wild and increased so much that, twenty-seven years afterwards, herds of

from 4000 to 8000 head were not uncommon. Cattle were afterwards taken

from this island to Mexico and to other parts of America, and in 1587,

sixty-five years after the conquest of Mexico, the Spaniards exported

64,350 hides from that country and 35,444 from St. Domingo, an

indication of the vast numbers of these animals which must then have

existed there, since those captured and killed could have been only a

small portion of the whole. In the pampas of Buenos Ayres there were, at

the end of the last century, about twelve million cows and three million

horses, besides great numbers in all other parts of America where open

pastures offered suitable conditions. Asses, about fifty years after

their introduction, ran wild and multiplied so amazingly in Quito, that

the Spanish traveller Ulloa describes them as being a nuisance. They

grazed together in great herds, defending themselves with their mouths,

and if a horse strayed among them they all fell upon him and did not

cease biting and kicking till they left him dead. Hogs were turned out

in St. Domingo by Columbus in 1493, and the Spaniards took them to other

places where they settled, the result being, that in about half a

century these animals were found in great numbers over a large part of

America, from 25Â° north to 40Â° south latitude. More recently, in New

Zealand, pigs have multiplied so greatly in a wild state as to be a

serious nuisance and injury to agriculture. To give some idea of their

numbers, it is stated that in the province of Nelson there were killed

in twenty months 25,000 wild pigs.[10] Now, in the case of all these

animals, we know that in their native countries, and even in America at

the present time, they do not increase at all in numbers; therefore the

whole normal increase must be kept down, year by year, by natural or

artificial means of destruction.

\_Rapid Increase and Wide Spread of Plants\_.

In the case of plants, the power of increase is even greater and its

effects more distinctly visible. Hundreds of square miles of the plains

of La Plata are now covered with two or three species of European

thistle, often to the exclusion of almost every other plant; but in the

native countries of these thistles they occupy, except in cultivated or

waste ground, a very subordinate part in the vegetation. Some American

plants, like the cotton-weed (Asclepias cuiussayica), have now become

common weeds over a large portion of the tropics. White clover

(Trifolium repens) spreads over all the temperate regions of the world,

and in New Zealand is exterminating many native species, including even

the native flax (Phormium tenax), a large plant with iris-like leaves 5

or 6 feet high. Mr. W.L. Travers has paid much attention to the effects

of introduced plants in New Zealand, and notes the following species as

being especially remarkable. The common knotgrass (Polygonum aviculare)

grows most luxuriantly, single plants covering a space 4 or 5 feet in

diameter, and sending their roots 3 or 4 feet deep. A large sub-aquatic

dock (Rumex obtusifolius) abounds in every river-bed, even far up among

the mountains. The common sow-thistle (Sonchus oleraceus) grows all over

the country up to an elevation of 6000 feet. The water-cress (Nasturtium

officinale) grows with amazing vigour in many of the rivers, forming

stems 12 feet long and 3/4 inch in diameter, and completely choking them

up. It cost Â£300 a year to keep the Avon at Christchurch free from it.

The sorrel (Rumex acetosella) covers hundreds of acres with a sheet of

red. It forms a dense mat, exterminating other plants, and preventing

cultivation. It can, however, be itself exterminated by sowing the

ground with red clover, which will also vanquish the Polygonum

aviculare. The most noxious weed in New Zealand appears, however, to be

the Hypochaeris radicata, a coarse yellow-flowered composite not

uncommon in our meadows and waste places. This has been introduced with

grass seeds from England, and is very destructive. It is stated that

excellent pasture was in three years destroyed by this weed, which

absolutely displaced every other plant on the ground. It grows in every

kind of soil, and is said even to drive out the white clover, which is

usually so powerful in taking possession of the soil.

In Australia another composite plant, called there the Cape-weed

(Cryptostemma calendulaceum), did much damage, and was noticed by Baron

Von Hugel in 1833 as "an unexterminable weed"; but, after forty years'

occupation, it was found to give way to the dense herbage formed by

lucerne and choice grasses.

In Ceylon we are told by Mr. Thwaites, in his \_Enumeration of Ceylon

Plants\_, that a plant introduced into the island less than fifty years

ago is helping to alter the character of the vegetation up to an

elevation of 3000 feet. This is the Lantana mixta, a verbenaceous plant

introduced from the West Indies, which appears to have found in Ceylon

a soil and climate exactly suited to it. It now covers thousands of

acres with its dense masses of foliage, taking complete possession of

land where cultivation has been neglected or abandoned, preventing the

growth of any other plants, and even destroying small trees, the tops of

which its subscandent stems are able to reach. The fruit of this plant

is so acceptable to frugivorous birds of all kinds that, through their

instrumentality, it is spreading rapidly, to the complete exclusion of

the indigenous vegetation where it becomes established.

\_Great Fertility not essential to Rapid Increase\_.

The not uncommon circumstance of slow-breeding animals being very

numerous, shows that it is usually the amount of destruction which an

animal or plant is exposed to, not its rapid multiplication, that

determines its numbers in any country. The passenger-pigeon (Ectopistes

migratorius) is, or rather was, excessively abundant in a certain area

in North America, and its enormous migrating flocks darkening the sky

for hours have often been described; yet this bird lays only two eggs.

The fulmar petrel exists in myriads at St. Kilda and other haunts of the

species, yet it lays only one egg. On the other hand the great shrike,

the tree-creeper, the nut-hatch, the nut-cracker, the hoopoe, and many

other birds, lay from four to six or seven eggs, and yet are never

abundant. So in plants, the abundance of a species bears little or no

relation to its seed-producing power. Some of the grasses and sedges,

the wild hyacinth, and many buttercups occur in immense profusion over

extensive areas, although each plant produces comparatively few seeds;

while several species of bell-flowers, gentians, pinks, and mulleins,

and even some of the composite, which produce an abundance of minute

seeds, many of which are easily scattered by the wind, are yet rare

species that never spread beyond a very limited area.

The above-mentioned passenger-pigeon affords such an excellent example

of an enormous bird-population kept up by a comparatively slow rate of

increase, and in spite of its complete helplessness and the great

destruction which it suffers from its numerous enemies, that the

following account of one of its breeding-places and migrations by the

celebrated American naturalist, Alexander Wilson, will be read with

interest:--

"Not far from Shelbyville, in the State of Kentucky, about five years

ago, there was one of these breeding-places, which stretched through the

woods in nearly a north and south direction, was several miles in

breadth, and was said to be upwards of 40 miles in extent. In this tract

almost every tree was furnished with nests wherever the branches could

accommodate them. The pigeons made their first appearance there about

the 10th of April, and left it altogether with their young before the

25th of May. As soon as the young were fully grown and before they left

the nests, numerous parties of the inhabitants from all parts of the

adjacent country came with waggons, axes, beds, cooking utensils, many

of them accompanied by the greater part of their families, and encamped

for several days at this immense nursery. Several of them informed me

that the noise was so great as to terrify their horses, and that it was

difficult for one person to hear another without bawling in his ear. The

ground was strewed with broken limbs of trees, eggs, and young squab

pigeons, which had been precipitated from above, and on which herds of

hogs were fattening. Hawks, buzzards, and eagles were sailing about in

great numbers, and seizing the squabs from the nests at pleasure; while,

from 20 feet upwards to the top of the trees, the view through the woods

presented a perpetual tumult of crowding and fluttering multitudes of

pigeons, their wings roaring like thunder, mingled with the frequent

crash of falling timber; for now the axemen were at work cutting down

those trees that seemed most crowded with nests, and contrived to fell

them in such a manner, that in their descent they might bring down

several others; by which means the falling of one large tree sometimes

produced 200 squabs little inferior in size to the old birds, and almost

one heap of fat. On some single trees upwards of a hundred nests were

found, each containing one squab only; a circumstance in the history of

the bird not generally known to naturalists.[11] It was dangerous to

walk under these flying and fluttering millions, from the frequent fall

of large branches, broken down by the weight of the multitudes above,

and which in their descent often destroyed numbers of the birds

themselves; while the clothes of those engaged in traversing the woods

were completely covered with the excrements of the pigeons.

"These circumstances were related to me by many of the most respectable

part of the community in that quarter, and were confirmed in part by

what I myself witnessed. I passed for several miles through this same

breeding-place, where every tree was spotted with nests, the remains of

those above described. In many instances I counted upwards of ninety

nests on a single tree; but the pigeons had abandoned this place for

another, 60 or 80 miles off, towards Green River, where they were said

at that time to be equally numerous. From the great numbers that were

constantly passing over our heads to or from that quarter, I had no

doubt of the truth of this statement. The mast had been chiefly consumed

in Kentucky; and the pigeons, every morning a little before sunrise, set

out for the Indiana territory, the nearest part of which was about sixty

miles distant. Many of these returned before ten o'clock, and the great

body generally appeared on their return a little after noon. I had left

the public road to visit the remains of the breeding-place near

Shelbyville, and was traversing the woods with my gun, on my way to

Frankfort, when about ten o'clock the pigeons which I had observed

flying the greater part of the morning northerly, began to return in

such immense numbers as I never before had witnessed. Coming to an

opening by the side of a creek, where I had a more uninterrupted view, I

was astonished at their appearance: they were flying with great

steadiness and rapidity, at a height beyond gunshot, in several strata

deep, and so close together that, could shot have reached them, one

discharge could not have failed to bring down several individuals. From

right to left, as far as the eye could reach, the breadth of this vast

procession extended, seeming everywhere equally crowded. Curious to

determine how long this appearance would continue, I took out my watch

to note the time, and sat down to observe them. It was then half-past

one; I sat for more than an hour, but instead of a diminution of this

prodigious procession, it seemed rather to increase, both in numbers and

rapidity; and anxious to reach Frankfort before night, I rose and went

on. About four o'clock in the afternoon I crossed Kentucky River, at the

town of Frankfort, at which time the living torrent above my head seemed

as numerous and as extensive as ever. Long after this I observed them in

large bodies that continued to pass for six or eight minutes, and these

again were followed by other detached bodies, all moving in the same

south-east direction, till after six o'clock in the evening. The great

breadth of front which this mighty multitude preserved would seem to

intimate a corresponding breadth of their breeding-place, which, by

several gentlemen who had lately passed through part of it, was stated

to me at several miles."

From these various observations, Wilson calculated that the number of

birds contained in the mass of pigeons which he saw on this occasion was

at least two thousand millions, while this was only one of many similar

aggregations known to exist in various parts of the United States. The

picture here given of these defenceless birds, and their still more

defenceless young, exposed to the attacks of numerous rapacious enemies,

brings vividly before us one of the phases of the unceasing struggle for

existence ever going on; but when we consider the slow rate of increase

of these birds, and the enormous population they are nevertheless able

to maintain, we must be convinced that in the case of the majority of

birds which multiply far more rapidly, and yet are never able to attain

such numbers, the struggle against their numerous enemies and against

the adverse forces of nature must be even more severe or more

continuous.

\_Struggle for Life between, closely allied Animals and Plants often the

most severe.\_

The struggle we have hitherto been considering has been mainly that

between an animal or plant and its direct enemies, whether these enemies

are other animals which devour it, or the forces of nature which destroy

it. But there is another kind of struggle often going on at the same

time between closely related species, which almost always terminates in

the destruction of one of them. As an example of what is meant, Darwin

states that the recent increase of the missel-thrush in parts of

Scotland has caused the decrease of the song-thrush.[12] The black rat

(Mus rattus) was the common rat of Europe till, in the beginning of the

eighteenth century, the large brown rat (Mus decumanus) appeared on the

Lower Volga, and thence spread more or less rapidly till it overran all

Europe, and generally drove out the black rat, which in most parts is

now comparatively rare or quite extinct. This invading rat has now been

carried by commerce all over the world, and in New Zealand has

completely extirpated a native rat, which the Maoris allege they brought

with them from their home in the Pacific; and in the same country a

native fly is being supplanted by the European house-fly. In Russia the

small Asiatic cockroach has driven away a larger native species; and in

Australia the imported hive-bee is exterminating the small stingless

native bee.

The reason why this kind of struggle goes on is apparent if we consider

that the allied species fill nearly the same place in the economy of

nature. They require nearly the same kind of food, are exposed to the

same enemies and the same dangers. Hence, if one has ever so slight an

advantage over the other in procuring food or in avoiding danger, in its

rapidity of multiplication or its tenacity of life, it will increase

more rapidly, and by that very fact will cause the other to decrease and

often become altogether extinct. In some cases, no doubt, there is

actual war between the two, the stronger killing the weaker; but this is

by no means necessary, and there may be cases in which the weaker

species, physically, may prevail, by its power of more rapid

multiplication, its better withstanding vicissitudes of climates, or its

greater cunning in escaping the attacks of the common enemies. The same

principle is seen at work in the fact that certain mountain varieties of

sheep will starve out other mountain varieties, so that the two cannot

be kept together. In plants the same thing occurs. If several distinct

varieties of wheat are sown together, and the mixed seed resown, some of

the varieties which best suit the soil and climate, or are naturally the

most fertile, will beat the others and so yield more seed, and will

consequently in a few years supplant the other varieties.

As an effect of this principle, we seldom find closely allied species

of animals or plants living together, but often in distinct though

adjacent districts where the conditions of life are somewhat different.

Thus we may find cowslips (Primula veris) growing in a meadow, and

primroses (P. vulgaris) in an adjoining wood, each in abundance, but not

often intermingled. And for the same reason the old turf of a pasture or

heath consists of a great variety of plants matted together, so much so

that in a patch little more than a yard square Mr. Darwin found twenty

distinct species, belonging to eighteen distinct genera and to eight

natural orders, thus showing their extreme diversity of organisation.

For the same reason a number of distinct grasses and clovers are sown in

order to make a good lawn instead of any one species; and the quantity

of hay produced has been found to be greater from a variety of very

distinct grasses than from any one species of grass.

It may be thought that forests are an exception to this rule, since in

the north-temperate and arctic regions we find extensive forests of

pines or of oaks. But these are, after all, exceptional, and

characterise those regions only where the climate is little favourable

to forest vegetation. In the tropical and all the warm temperate parts

of the earth, where there is a sufficient supply of moisture, the

forests present the same variety of species as does the turf of our old

pastures; and in the equatorial virgin forests there is so great a

variety of forms, and they are so thoroughly intermingled, that the

traveller often finds it difficult to discover a second specimen of any

particular species which he has noticed. Even the forests of the

temperate zones, in all favourable situations, exhibit a considerable

variety of trees of distinct genera and families, and it is only when we

approach the outskirts of forest vegetation, where either drought or

winds or the severity of the winter is adverse to the existence of most

trees, that we find extensive tracts monopolised by one or two species.

Even Canada has more than sixty different forest trees and the Eastern

United States a hundred and fifty; Europe is rather poor, containing

about eighty trees only; while the forests of Eastern Asia, Japan, and

Manchuria are exceedingly rich, about a hundred and seventy species

being already known. And in all these countries the trees grow

intermingled, so that in every extensive forest we have a considerable

variety, as may be seen in the few remnants of our primitive woods in

some parts of Epping Forest and the New Forest.

Among animals the same law prevails, though, owing to their constant

movements and power of concealment, it is not so readily observed. As

illustrations we may refer to the wolf, ranging over Europe and Northern

Asia, while the jackal inhabits Southern Asia and Northern Africa; the

tree-porcupines, of which there are two closely allied species, one

inhabiting the eastern, the other the western half of North America; the

common hare (Lepus timidus) in Central and Southern Europe, while all

Northern Europe is inhabited by the variable hare (Lepus variabilis);

the common jay (Garrulus glandarius) inhabiting all Europe, while

another species (Garrulus Brandti) is found all across Asia from the

Urals to Japan; and many species of birds in the Eastern United States

are replaced by closely allied species in the west. Of course there are

also numbers of closely related species in the same country, but it will

almost always be found that they frequent different stations and have

somewhat different habits, and so do not come into direct competition

with each other; just as closely allied plants may inhabit the same

districts, when one prefers meadows the other woods, one a chalky soil

the other sand, one a damp situation the other a dry one. With plants,

fixed as they are to the earth, we easily note these peculiarities of

station; but with wild animals, which we see only on rare occasions, it

requires close and long-continued observation to detect the

peculiarities in their mode of life which may prevent all direct

competition between closely allied species dwelling in the same area.

\_The Ethical Aspect of the Struggle for Existence\_.

Our exposition of the phenomena presented by the struggle for existence

may be fitly concluded by a few remarks on its ethical aspect. Now that

the war of nature is better known, it has been dwelt upon by many

writers as presenting so vast an amount of cruelty and pain as to be

revolting to our instincts of humanity, while it has proved a

stumbling-block in the way of those who would fain believe in an

all-wise and benevolent ruler of the universe. Thus, a brilliant writer

says: "Pain, grief, disease, and death, are these the inventions of a

loving God? That no animal shall rise to excellence except by being

fatal to the life of others, is this the law of a kind Creator? It is

useless to say that pain has its benevolence, that massacre has its

mercy. Why is it so ordained that bad should be the raw material of

good? Pain is not the less pain because it is useful; murder is not less

murder because it is conducive to development. Here is blood upon the

hand still, and all the perfumes of Arabia will not sweeten it."[13]

Even so thoughtful a writer as Professor Huxley adopts similar views. In

a recent article on "The Struggle for Existence" he speaks of the

myriads of generations of herbivorous animals which "have been tormented

and devoured by carnivores"; of the carnivores and herbivores alike

"subject to all the miseries incidental to old age, disease, and

over-multiplication"; and of the "more or less enduring suffering,"

which is the meed of both vanquished and victor. And he concludes that,

since thousands of times a minute, were our ears sharp enough, we should

hear sighs and groans of pain like those heard by Dante at the gate of

hell, the world cannot be governed by what we call benevolence.[14]

Now there is, I think, good reason to believe that all this is greatly

exaggerated; that the supposed "torments" and "miseries" of animals have

little real existence, but are the reflection of the imagined sensations

of cultivated men and women in similar circumstances; and that the

amount of actual suffering caused by the struggle for existence among

animals is altogether insignificant. Let us, therefore, endeavour to

ascertain what are the real facts on which these tremendous accusations

are founded.

In the first place, we must remember that animals are entirely spared

the pain we suffer in the anticipation of death--a pain far greater, in

most cases, than the reality. This leads, probably, to an almost

perpetual enjoyment of their lives; since their constant watchfulness

against danger, and even their actual flight from an enemy, will be the

enjoyable exercise of the powers and faculties they possess, unmixed

with any serious dread. There is, in the next place, much evidence to

show that violent deaths, if not too prolonged, are painless and easy;

even in the case of man, whose nervous system is in all probability much

more susceptible to pain than that of most animals. In all cases in

which persons have escaped after being seized by a lion or tiger, they

declare that they suffered little or no pain, physical or mental. A

well-known instance is that of Livingstone, who thus describes his

sensations when seized by a lion: "Starting and looking half round, I

saw the lion just in the act of springing on me. I was upon a little

height; he caught my shoulder as he sprang, and we both came to the

ground below together. Growling horribly close to my ear, he shook me as

a terrier-dog does a rat. The shock produced a stupor similar to that

which seems to be felt by a mouse after the first shake of the cat. It

causes a sort of dreaminess, \_in which there was no sense of pain or

feeling of terror\_, though I was quite conscious of all that was

happening. It was like what patients partially under the influence of

chloroform describe, who see all the operation, but feel not the knife.

This singular condition was not the result of any mental process. The

shake annihilated fear, and allowed no sense of horror in looking round

at the beast."

This absence of pain is not peculiar to those seized by wild beasts, but

is equally produced by any accident which causes a general shock to the

system. Mr. Whymper describes an accident to himself during one of his

preliminary explorations of the Matterhorn, when he fell several hundred

feet, bounding from rock to rock, till fortunately embedded in a

snow-drift near the edge of a tremendous precipice. He declares that

while falling and feeling blow after blow, he neither lost consciousness

nor suffered pain, merely thinking, calmly, that a few more blows would

finish him. We have therefore a right to conclude, that when death

follows soon after any great shock it is as easy and painless a death as

possible; and this is certainly what happens when an animal is seized by

a beast of prey. For the enemy is one which hunts for food, not for

pleasure or excitement; and it is doubtful whether any carnivorous

animal in a state of nature begins to seek after prey till driven to do

so by hunger. When an animal is caught, therefore, it is very soon

devoured, and thus the first shock is followed by an almost painless

death. Neither do those which die of cold or hunger suffer much. Cold is

generally severest at night and has a tendency to produce sleep and

painless extinction. Hunger, on the other hand, is hardly felt during

periods of excitement, and when food is scarce the excitement of seeking

for it is at its greatest. It is probable, also, that when hunger

presses, most animals will devour anything to stay their hunger, and

will die of gradual exhaustion and weakness not necessarily painful, if

they do not fall an earlier prey to some enemy or to cold.[15]

Now let us consider what are the enjoyments of the lives of most

animals. As a rule they come into existence at a time of year when food

is most plentiful and the climate most suitable, that is in the spring

of the temperate zone and at the commencement of the dry season in the

tropics. They grow vigorously, being supplied with abundance of food;

and when they reach maturity their lives are a continual round of

healthy excitement and exercise, alternating with complete repose. The

daily search for the daily food employs all their faculties and

exercises every organ of their bodies, while this exercise leads to the

satisfaction of all their physical needs. In our own case, we can give

no more perfect definition of happiness, than this exercise and this

satisfaction; and we must therefore conclude that animals, as a rule,

enjoy all the happiness of which they are capable. And this normal state

of happiness is not alloyed, as with us, by long periods--whole lives

often--of poverty or ill-health, and of the unsatisfied longing for

pleasures which others enjoy but to which we cannot attain. Illness, and

what answers to poverty in animals--continued hunger--are quickly

followed by unanticipated and almost painless extinction. Where we err

is, in giving to animals feelings and emotions which they do not

possess. To us the very sight of blood and of torn or mangled limbs is

painful, while the idea of the suffering implied by it is heartrending.

We have a horror of all violent and sudden death, because we think of

the life full of promise cut short, of hopes and expectations

unfulfilled, and of the grief of mourning relatives. But all this is

quite out of place in the case of animals, for whom a violent and a

sudden death is in every way the best. Thus the poet's picture of

"Nature red in tooth and claw

With ravine"

is a picture the evil of which is read into it by our imaginations, the

reality being made up of full and happy lives, usually terminated by the

quickest and least painful of deaths.

On the whole, then, we conclude that the popular idea of the struggle

for existence entailing misery and pain on the animal world is the very

reverse of the truth. What it really brings about, is, the maximum of

life and of the enjoyment of life with the minimum of suffering and

pain. Given the necessity of death and reproduction--and without these

there could have been no progressive development of the organic

world,--and it is difficult even to imagine a system by which a greater

balance of happiness could have been secured. And this view was

evidently that of Darwin himself, who thus concludes his chapter on the

struggle for existence: "When we reflect on this struggle, we may

console ourselves with the full belief that the war of nature is not

incessant, that no fear is felt, that death is generally prompt, and

that the vigorous, the healthy, and the happy survive and multiply."

FOOTNOTES:

[Footnote 4: \_GÃ©ographic Botanique\_, p. 798.]

[Footnote 5: \_The Origin of Species\_, p. 53.]

[Footnote 6: \_The Earth as Modified by Human Action\_, p. 51.]

[Footnote 7: \_The Origin of Species\_, p. 56.]

[Footnote 8: See \_Nature\_, vol. xxxi. p. 63.]

[Footnote 9: \_A Visit to South America\_, 1878; also \_Nature\_, vol. xxxi.

pp. 263-339.]

[Footnote 10: Still more remarkable is the increase of rabbits both in

New Zealand and Australia. No less than seven millions of rabbit-skins

have been exported from the former country in a single year, their value

being Â£67,000. In both countries, sheep-runs have been greatly

deteriorated in value by the abundance of rabbits, which destroy the

herbage; and in some cases they have had to be abandoned altogether.]

[Footnote 11: Later observers have proved that two eggs are laid and

usually two young produced, but it may be that in most cases only one of

these comes to maturity.]

[Footnote 12: \_Origin of Species\_, p. 59. Professor A. Newton, however,

informs me that these species do not interfere with one another in the

way here stated.]

[Footnote 13: Winwood Reade's \_Martyrdom of Man,\_ p. 520.]

[Footnote 14: \_Nineteenth Century,\_ February 1888, pp. 162, 163.]

[Footnote 15: The Kestrel, which usually feeds on mice, birds, and

frogs, sometimes stays its hunger with earthworms, as do some of the

American buzzards. The Honey-buzzard sometimes eats not only earthworms

and slugs, but even corn; and the Buteo borealis of North America, whose

usual food is small mammals and birds, sometimes eats crayfish.]

CHAPTER III

THE VARIABILITY OF SPECIES IN A STATE OF NATURE

Importance of variability--Popular ideas regarding

it--Variability of the lower animals--The variability of

insects--Variation among lizards--Variation among

birds--Diagrams of bird-variation--Number of varying

individuals--Variation in the mammalia--Variation in internal

organs--Variations in the skull--Variations in the habits of

Animals--The Variability of plants--Species which vary

little--Concluding remarks.

The foundation of the Darwinian theory is the variability of species,

and it is quite useless to attempt even to understand that theory, much

less to appreciate the completeness of the proof of it, unless we first

obtain a clear conception of the nature and extent of this variability.

The most frequent and the most misleading of the objections to the

efficacy of natural selection arise from ignorance of this subject, an

ignorance shared by many naturalists, for it is only since Mr. Darwin

has taught us their importance that varieties have been systematically

collected and recorded; and even now very few collectors or students

bestow upon them the attention they deserve. By the older naturalists,

indeed, varieties--especially if numerous, small, and of frequent

occurrence--were looked upon as an unmitigated nuisance, because they

rendered it almost impossible to give precise definitions of species,

then considered the chief end of systematic natural history. Hence it

was the custom to describe what was supposed to be the "typical form" of

species, and most collectors were satisfied if they possessed this

typical form in their cabinets. Now, however, a collection is valued in

proportion as it contains illustrative specimens of all the varieties

that occur in each species, and in some cases these have been carefully

described, so that we possess a considerable mass of information on the

subject. Utilising this information we will now endeavour to give some

idea of the nature and extent of variation in the species of animals and

plants.

It is very commonly objected that the widespread and constant

variability which is admitted to be a characteristic of domesticated

animals and cultivated plants is largely due to the unnatural conditions

of their existence, and that we have no proof of any corresponding

amount of variation occurring in a state of nature. Wild animals and

plants, it is said, are usually stable, and when variations occur these

are alleged to be small in amount and to affect superficial characters

only; or if larger and more important, to occur so rarely as not to

afford any aid in the supposed formation of new species.

This objection, as will be shown, is utterly unfounded; but as it is one

which goes to the very root of the problem, it is necessary to enter at

some length into the various proofs of variation in a state of nature.

This is the more necessary because the materials collected by Mr. Darwin

bearing on this question have never been published, and comparatively

few of them have been cited in \_The Origin of Species\_; while a

considerable body of facts has been made known since the publication of

the last edition of that work.

\_Variability of the Lower Animals\_.

Among the lowest and most ancient marine organisms are the Foraminifera,

little masses of living jelly, apparently structureless, but which

secrete beautiful shelly coverings, often perfectly symmetrical, as

varied in form as those of the mollusca and far more complicated. These

have been studied with great care by many eminent naturalists, and the

late Dr. W.B. Carpenter in his great work--the \_Introduction to the

Study of the Foraminifera\_--thus refers to their variability: "There is

not a single species of plant or animal of which the range of variation

has been studied by the collocation and comparison of so large a number

of specimens as have passed under the review of Messrs. Williamson,

Parker, Rupert Jones, and myself in our studies of the types of this

group;" and he states as the result of this extensive comparison of

specimens: "The range of variation is so great among the Foraminifera

as to include not merely those differential characters which have been

usually accounted \_specific\_, but also those upon which the greater part

of the \_genera\_, of this group have been founded, and even in some

instances those of its \_orders\_."[16]

Coming now to a higher group--the Sea-Anemones--Mr. P.H. Gosse and other

writers on these creatures often refer to variations in size, in the

thickness and length of the tentacles, the form of the disc and of the

mouth, and the character of surface of the column, while the colour

varies enormously in a great number of the species. Similar variations

occur in all the various groups of marine invertebrata, and in the great

sub-kingdom of the mollusca they are especially numerous. Thus, Dr. S.P.

Woodward states that many present a most perplexing amount of variation,

resulting (as he supposes) from supply of food, variety of depth and of

saltness of the water; but we know that many variations are quite

independent of such causes, and we will now consider a few cases among

the land-mollusca in which they have been more carefully studied.

In the small forest region of Oahu, one of the Sandwich Islands, there

have been found about 175 species of land-shells represented by 700 or

800 varieties; and we are told by the Rev. J.T. Gulick, who studied them

carefully, that "we frequently find a genus represented in several

successive valleys by allied species, sometimes feeding on the same,

sometimes on different plants. In every such case the valleys that are

nearest to each other furnish the most nearly allied forms; \_and a full

set of the varieties of each species presents a minute gradation of

forms between the more divergent types found in the more widely

separated localities\_."

In most land-shells there is a considerable amount of variation in

colour, markings, size, form, and texture or striation of the surface,

even in specimens collected in the same locality. Thus, a French author

has enumerated no less than 198 varieties of the common wood-snail

(Helix nemoralis), while of the equally common garden-snail (Helix

hortensis) ninety varieties have been described. Fresh-water shells are

also subject to great variation, so that there is much uncertainty as

to the number of species; and variations are especially frequent in the

Planorbidae, which exhibit many eccentric deviations from the usual form

of the species--deviations which must often affect the form of the

living animal. In Mr. Ingersoll's Report on the Recent Mollusca of

Colorado many of these extraordinary variations are referred to, and it

is stated that a shell (Helisonia trivolvis) abundant in some small

ponds and lakes, had scarcely two specimens alike, and many of them

closely resembled other and altogether distinct species.[17]

\_The Variability of Insects\_.

Among Insects there is a large amount of variation, though very few

entomologists devote themselves to its investigation. Our first examples

will be taken from the late Mr. T. Vernon Wollaston's book, \_On the

Variation of Species\_, and they must be considered as indications of

very widespread though little noticed phenomena. He speaks of the

curious little carabideous beetles of the genus Notiophilus as being

"extremely unstable both in their sculpture and hue;" of the common

Calathus mollis as having "the hind wings at one time ample, at another

rudimentary, and at a third nearly obsolete;" and of the same

irregularity as to the wings being characteristic of many Orthoptera and

of the Homopterous Fulgoridae. Mr. Westwood in his \_Modern

Classification of Insects\_ states that "the species of Gerris,

Hydrometra, and Velia are mostly found perfectly apterous, though

occasionally with full-sized wings."

It is, however, among the Lepidoptera (butterflies and moths) that the

most numerous cases of variation have been observed, and every good

collection of these insects affords striking examples. I will first

adduce the testimony of Mr. Bates, who speaks of the butterflies of the

Amazon valley exhibiting innumerable local varieties or races, while

some species showed great individual variability. Of the beautiful

Mechanitis Polymnia he says, that at Ega on the Upper Amazons, "it

varies not only in general colour and pattern, but also very

considerably in the shape of the wings, especially in the male sex."

Again, at St. Paulo, Ithomia Orolina exhibits four distinct varieties,

all occurring together, and these differ not only in colour but in form,

one variety being described as having the fore wings much elongated in

the male, while another is much larger and has "the hind wings in the

male different in shape." Of Heliconius Numata Mr. Bates says: "This

species is so variable that it is difficult to find two examples exactly

alike," while "it varies in structure as well as in colours. The wings

are sometimes broader, sometimes narrower; and their edges are simple in

some examples and festooned in others." Of another species of the same

genus, H. melpomene, ten distinct varieties are described all more or

less connected by intermediate forms, and four of these varieties were

obtained at one locality, Serpa on the north bank of the Amazon.

Ceratina Ninonia is another of these very unstable species exhibiting

many local varieties which are, however, incomplete and connected by

intermediate forms; while the several species of the genus Lycorea all

vary to such an extent as almost to link them together, so that Mr.

Bates thinks they might all fairly be considered as varieties of one

species only.

Turning to the Eastern Hemisphere we have in Papilio Severus a species

which exhibits a large amount of simple variation, in the presence or

absence of a pale patch on the upper wings, in the brown submarginal

marks on the lower wings, in the form and extent of the yellow band, and

in the size of the specimens. The most extreme forms, as well as the

intermediate ones, are often found in one locality and in company with

each other. A small butterfly (Terias hecabe) ranges over the whole of

the Indian and Malayan regions to Australia, and everywhere exhibits

great variations, many of which have been described as distinct species;

but a gentleman in Australia bred two of these distinct forms (T. hecabe

and T. Aesiope), with several intermediates, from one batch of

caterpillars found feeding together on the same plant.[18] It is

therefore very probable that a considerable number of supposed distinct

species are only individual varieties.

Cases of variation similar to those now adduced among butterflies might

be increased indefinitely, but it is as well to note that such important

characters as the neuration of the wings, on which generic and family

distinctions are often established, are also subject to variation. The

Rev. R.P. Murray, in 1872, laid before the Entomological Society

examples of such variation in six species of butterflies, and other

cases have been since described. The larvae of butterflies and moths are

also very variable, and one observer recorded in the \_Proceedings of the

Entomological Society for\_ 1870 no less than sixteen varieties of the

caterpillar of the bedstraw hawk-moth (Deilephela galii).

\_Variation among Lizards\_.

Passing on from the lower animals to the vertebrata, we find more

abundant and more definite evidence as to the extent and amount of

individual variation. I will first give a case among the Reptilia from

some of Mr. Darwin's unpublished MSS., which have been kindly lent me by

Mr. Francis Darwin.

"M. Milne Edwards (\_Annales des Sci. Nat.\_, I ser., tom. xvi. p. 50) has

given a curious table of measurements of fourteen specimens of Lacerta

muralis; and, taking the length of the head as a standard, he finds the

neck, trunk, tail, front and hind legs, colour, and femoral pores, all

varying wonderfully; and so it is more or less with other species. So

apparently trifling a character as the scales on the head affording

almost the only constant characters."

[Illustration: FIG. 1.--Variations of Lacerta muralis.]

[Illustration: FIG. 2.--Variation of Lizards.]

As the table of measurements above referred to would give no clear

conception of the nature and amount of the variation without a laborious

study and comparison of the figures, I have endeavoured to find a method

of presenting the facts to the eye, so that they may be easily grasped

and appreciated. In the diagram opposite, the comparative variations of

the different organs of this species are given by means of variously

bent lines. The head is represented by a straight line because it

presented (apparently) no variation. The body is next given, the

specimens being arranged in the order of their size from No. 1, the

smallest, to No. 14, the largest, the actual lengths being laid down

from a base line at a suitable distance below, in this case two inches

below the centre, the mean length of the body of the fourteen specimens

being two inches. The respective lengths of the neck, legs, and toe of

each specimen are then laid down in the same manner at convenient

distances apart for comparison; and we see that their variations bear no

definite relation to those of the body, and not much to those of each

other. With the exception of No. 5, in which all the parts agree in

being large, there is a marked independence of each part, shown by the

lines often curving in opposite directions; which proves that in those

specimens one part is large while the other is small. The actual amount

of the variation is very great, ranging from one-sixth of the mean

length in the neck to considerably more than a fourth in the hind leg,

and this among only fourteen examples which happen to be in a particular

museum.

To prove that this is not an isolated case, Professor Milne Edwards also

gives a table showing the amount of variation in the museum specimens of

six common species of lizards, also taking the head as the standard, so

that the comparative variation of each part to the head is given. In the

accompanying diagram (Fig. 2) the variations are exhibited by means of

lines of varying length. It will be understood that, however much the

specimens varied in \_size\_, if they had kept the same \_proportions\_, the

variation line would have been in every case reduced to a point, as in

the neck of L. velox which exhibits no variation. The different

proportions of the variation lines for each species may show a distinct

mode of variation, or may be merely due to the small and differing

number of specimens; for it is certain that whatever amount of variation

occurs among a few specimens will be greatly increased when a much

larger number of specimens are examined. That the amount of variation is

large, may be seen by comparing it with the actual length of the head

(given below the diagram) which was used as a standard in determining

the variation, but which itself seems not to have varied.[19]

\_Variation among Birds\_.

Coming now to the class of Birds, we find much more copious evidence of

variation. This is due partly to the fact that Ornithology has perhaps a

larger body of devotees than any other branch of natural history (except

entomology); to the moderate size of the majority of birds; and to the

circumstance that the form and dimensions of the wings, tail, beak, and

feet offer the best generic and specific characters and can all be

easily measured and compared. The most systematic observations on the

individual variation of birds have been made by Mr. J.A. Allen, in his

remarkable memoir: "On the Mammals and Winter Birds of East Florida,

with an examination of certain assumed specific characters in Birds, and

a sketch of the Bird Faunae of Eastern North America," published in the

\_Bulletin of the Museum of Comparative Zoology\_ at Harvard College,

Cambridge, Massachusetts, in 1871. In this work exact measurements are

given of all the chief external parts of a large number of species of

common American birds, from twenty to sixty or more specimens of each

species being measured, so that we are able to determine with some

precision the nature and extent of the variation that usually occurs.

Mr. Allen says: "The facts of the case show that a variation of from 15

to 20 per cent in general size, and an equal degree of variation in the

relative size of different parts, may be ordinarily expected among

specimens of the same species and sex, taken at the same locality, while

in some cases the variation is even greater than this." He then goes on

to show that each part varies to a considerable extent independently of

the other parts; so that when the size varies, the proportions of all

the parts vary, often to a much greater amount. The wing and tail, for

example, besides varying in length, vary in the proportionate length of

each feather, and this causes their outline to vary considerably in

shape. The bill also varies in length, width, depth, and curvature. The

tarsus varies in length, as does each toe separately and independently;

and all this not to a minute degree requiring very careful measurement

to detect it at all, but to an amount easily seen without any

measurement, as it averages one-sixth of the whole length and often

reaches one-fourth. In twelve species of common perching birds the wing

varied (in from twenty-five to thirty specimens) from 14 to 21 per cent

of the mean length, and the tail from 13.8 to 23.4 per cent. The

variation of the form of the wing can be very easily tested by noting

which feather is longest, which next in length, and so on, the

respective feathers being indicated by the numbers 1, 2, 3, etc.,

commencing with the outer one. As an example of the irregular variation

constantly met with, the following occurred among twenty-five specimens

of Dendroeca coronata. Numbers bracketed imply that the corresponding

feathers were of equal length.[20]

RELATIVE LENGTHS OF PRIMARY WING FEATHERS OF

DENDROECA CORONATA.

---------+-----------+----------+-----------+----------+----------

Longest. | Second in | Third in | Fourth in | Fifth in | Sixth in

| Length. | Length. | Length. | Length. | Length.

---------+-----------+----------+-----------+----------+----------

2 | 3 | 1 | 4 | 5 | 6

3 | 2 | 4 | 1 | 5 | 6

| / 2 | | | |

3 | { | 1 | 5 | 6 | 7

| \ 4 | | | |

2 \ | | | | |

} | 4 | 1 | 5 | 6 | 7

3 / | | | | |

2 \ | | | | |

1 | | | | | |

} | 5 | 6 | 7 | 8 | 9

3 | | | | | |

4 / | | | | |

---------+-----------+----------+-----------+----------+----------

Here we have five very distinct proportionate lengths of the wing

feathers, any one of which is often thought sufficient to characterise a

distinct species of bird; and though this is rather an extreme case, Mr.

Allen assures us that "the comparison, extended in the table to only a

few species, has been carried to scores of others with similar results."

Along with this variation in size and proportions there occurs a large

amount of variation in colour and markings. "The difference in intensity

of colour between the extremes of a series of fifty or one hundred

specimens of any species, collected at a single locality, and nearly at

the same season of the year, is often as great as occurs between truly

distinct species." But there is also a great amount of individual

variability in the markings of the same species. Birds having the

plumage varied with streaks and spots differ exceedingly in different

individuals of the same species in respect to the size, shape, and

number of these marks, and in the general aspect of the plumage

resulting from such variations. "In the common song sparrow (Melospiza

melodia), the fox-coloured sparrow (Passerella iliaca), the swamp

sparrow (Melospiza palustris), the black and white creeper (Mniotilta

varia), the water-wagtail (Seiurus novaeboracencis), in Turdus

fuscescens and its allies, the difference in the size of the streaks is

often very considerable. In the song sparrow they vary to such an extent

that in some cases they are reduced to narrow lines; in others so

enlarged as to cover the greater part of the breast and sides of the

body, sometimes uniting on the middle of the breast into a nearly

continuous patch."

Mr. Allen then goes on to particularise several species in which such

variations occur, giving cases in which two specimens taken at the same

place on the same day exhibited the two extremes of coloration. Another

set of variations is thus described: "The white markings so common on

the wings and tails of birds, as the bars formed by the white tips of

the greater wing-coverts, the white patch occasionally present at the

base of the primary quills, or the white band crossing them, and the

white patch near the end of the outer tail-feathers are also extremely

liable to variation in respect to their extent and the number of

feathers to which, in the same species, these markings extend." It is to

be especially noted that all these varieties are distinct from those

which depend on season, on age, or on sex, and that they are such as

have in many other species been considered to be of specific value.

These variations of colour could not be presented to the eye without a

series of carefully engraved plates, but in order to bring Mr. Allen's

\_measurements\_, illustrating variations of size and proportion, more

clearly before the reader, I have prepared a series of diagrams

illustrating the more important facts and their bearings on the

Darwinian theory.

The first of these is intended, mainly, to show the actual amount of the

variation, as it gives the true length of the wing and tail in the

extreme cases among thirty specimens of each of three species. The

shaded portion shows the minimum length, the unshaded portion the

additional length in the maximum. The point to be specially noted here

is, that in each of these common species there is about the same amount

of variation, and that it is so great as to be obvious at a glance.

[Illustration: FIG. 3.--Variation of Wings and Tail.]

There is here no question of "minute" or "infinitesimal" variation,

which many people suppose to be the only kind of variation that exists.

It cannot even be called small; yet from all the evidence we now possess

it seems to be the amount which characterises most of the common species

of birds.

It may be said, however, that these are the extreme variations, and only

occur in one or two individuals, while the great majority exhibit little

or no difference. Other diagrams will show that this is not the case;

but even if it were so, it would be no objection at all, because these

are the extremes among thirty specimens only. We may safely assume that

these thirty specimens, taken by chance, are not, in the case of all

these species, exceptional lots, and therefore we might expect at least

two similarly varying specimens in each additional thirty. But the

number of individuals, even in a very rare species, is probably thirty

thousand or more, and in a common species thirty, or even three hundred,

millions. Even one individual in each thirty, varying to the amount

shown in the diagram, would give at least a million in the total

population of any common bird, and among this million many would vary

much more than the extreme among thirty only. We should thus have a vast

body of individuals varying to a large extent in the length of the wings

and tail, and offering ample material for the modification of these

organs by natural selection. We will now proceed to show that other

parts of the body vary, simultaneously, but independently, to an equal

amount.

[Illustration: FIG. 4.--Dolichonyx oryzivorus. 20 Males.]

[Illustration: FIG. 5.--Agelaeus phoeniceus. 40 Males.]

The first bird taken is the common Bob-o-link or Rice-bird (Dolichonyx

oryzivorus), and the Diagram, Fig. 4, exhibits the variations of seven

important characters in twenty male adult specimens.[21] These

characters are--the lengths of the body, wing, tail, tarsus, middle toe,

outer toe, and hind toe, being as many as can be conveniently exhibited

in one diagram. The length of the body is not given by Mr. Allen, but as

it forms a convenient standard of comparison, it has been obtained by

deducting the length of the tail from the total length of the birds as

given by him. The diagram has been constructed as follows:--The twenty

specimens are first arranged in a series according to the body-lengths

(which may be considered to give the size of the bird), from the

shortest to the longest, and the same number of vertical lines are

drawn, numbered from one to twenty. In this case (and wherever

practicable) the body-length is measured from the lower line of the

diagram, so that the actual length of the bird is exhibited as well as

the actual variations of length. These can be well estimated by means of

the horizontal line drawn at the mean between the two extremes, and it

will be seen that one-fifth of the total number of specimens taken on

either side exhibits a very large amount of variation, which would of

course be very much greater if a hundred or more specimens were

compared. The lengths of the wing, tail, and other parts are then laid

down, and the diagram thus exhibits at a glance the comparative

variation of these parts in every specimen as well as the actual amount

of variation in the twenty specimens; and we are thus enabled to arrive

at some important conclusions.

We note, first, that the variations of none of the parts follow the

variations of the body, but are sometimes almost in an opposite

direction. Thus the longest wing corresponds to a rather small body, the

longest tail to a medium body, while the longest leg and toes belong to

only a moderately large body. Again, even related parts do not

constantly vary together but present many instances of independent

variation, as shown by the want of parallelism in their respective

variation-lines. In No. 5 (see Fig. 4) the wing is very long, the tail

moderately so; while in No. 6 the wing is much shorter while the tail is

considerably longer. The tarsus presents comparatively little variation;

and although the three toes may be said to vary in general together,

there are many divergencies; thus, in passing from No. 9 to No. 10, the

outer toe becomes longer, while the hind toe becomes considerably

shorter; while in Nos. 3 and 4 the middle toe varies in an opposite way

to the outer and the hind toes.

[Illustration: FIG. 6.--Cardinalis virginianus. 31 Males.]

In the next diagram (Fig. 5) we have the variations in forty males of

the Red-winged Blackbird (Agelaeus phoeniceus), and here we see the same

general features. One-fifth of the whole number of specimens offer a

large amount of variation either below or above the mean; while the

wings, tail, and head vary quite independently of the body. The wing and

tail too, though showing some amount of correlated variation, yet in

no less than nine cases vary in opposite directions as compared with the

preceding species.

The next diagram (Fig. 6), showing the variations of thirty-one males of

the Cardinal bird (Cardinalis virginianus), exhibits these features much

more strongly. The amount of variation in proportion to the size of the

bird is very much greater; while the variations of the wing and tail not

only have no correspondence with that of the body but very little with

each other. In no less than twelve or thirteen instances they vary in

opposite directions, while even where they correspond in direction the

amount of the variation is often very disproportionate.

As the proportions of the tarsi and toes of birds have great influence

on their mode of life and habits and are often used as specific or even

generic characters, I have prepared a diagram (Fig. 7) to show the

variation in these parts only, among twenty specimens of each of four

species of birds, four or five of the most variable alone being given.

The extreme divergence of each of the lines in a vertical direction

shows the actual amount of variation; and if we consider the small

length of the toes of these small birds, averaging about three-quarters

of an inch, we shall see that the variation is really very large; while

the diverging curves and angles show that each part varies, to a great

extent, independently. It is evident that if we compared some thousands

of individuals instead of only twenty, we should have an amount of

independent variation occurring each year which would enable almost any

modification of these important organs to be rapidly effected.

[Illustration: FIG. 7.--Variation of Tarsus and Toes.]

[Illustration: FIG. 8.--Variation of Birds in Leyden Museum.]

In order to meet the objection that the large amount of variability here

shown depends chiefly on the observations of one person and on the birds

of a single country, I have examined Professor Schlegel's Catalogue of

the Birds in the Leyden Museum, in which he usually gives the range of

variation of the specimens in the museum (which are commonly less than a

dozen and rarely over twenty) as regards some of their more important

dimensions. These fully support the statement of Mr. Allen, since they

show an equal amount of variability when the numbers compared are

sufficient, which, however, is not often the case. The accompanying

diagram exhibits the actual differences of size in five organs which

occur in five species taken almost at random from this catalogue. Here,

again, we perceive that the variation is decidedly large, even among a

very small number of specimens; while the facts all show that there is

no ground whatever for the common assumption that natural species

consist of individuals which are nearly all alike, or that the

variations which occur are "infinitesimal" or even "small."

\_The proportionate Number of Individuals which present a considerable

amount of Variation.\_

The notion that variation is a comparatively exceptional phenomenon, and

that in any case considerable variations occur very rarely in proportion

to the number of individuals which do not vary, is so deeply rooted that

it is necessary to show by every possible method of illustration how

completely opposed it is to the facts of nature. I have therefore

prepared some diagrams in which each of the individual birds measured is

represented by a spot, placed at a proportionate distance, right and

left, from the median line accordingly as it varies in excess or defect

of the mean length as regards the particular part compared. As the

object in this set of diagrams is to show the number of individuals

which vary considerably in proportion to those which vary little or not

at all, the scale has been enlarged in order to allow room for placing

the spots without overlapping each other.

In the diagram opposite twenty males of Icterus Baltimore are

registered, so as to exhibit to the eye the proportionate number of

specimens which vary, to a greater or less amount, in the length of the

tail, wing, tarsus, middle toe, hind toe, and bill. It will be noticed

that there is usually no very great accumulation of dots about the

median line which shows the average dimensions, but that a considerable

number are spread at varying distances on each side of it.

In the next diagram (Fig. 10), showing the variation among forty males

of Agelaeeus phoeniceus, this approach to an equable spreading of the

variations is still more apparent; while in Fig. 12, where fifty-eight

specimens of Cardinalis virginianus are registered, we see a remarkable

spreading out of the spots, showing in some of the characters a tendency

to segregation into two or more groups of individuals, each varying

considerably from the mean.

[Illustration: FIG. 9]

[Illustration: FIG. 10.]

[Illustration: FIG. 11.]

In order fully to appreciate the teaching of these diagrams, we must

remember, that, whatever kind and amount of variations are exhibited by

the few specimens here compared, would be greatly extended and brought

into symmetrical form if large numbers--thousands or millions--were

subjected to the same process of measurement and registration. We know,

from the general law which governs variations from a mean value, that

with increasing numbers the range of variation of each part would

increase also, at first rather rapidly and then more slowly; while gaps

and irregularities would be gradually filled up, and at length the

distribution of the dots would indicate a tolerably regular curve of

double curvature like those shown in Fig. 11. The great divergence of

the dots, when even a few specimens are compared, shows that the curve,

with high numbers, would be a flat one like the lower curve in the

illustration here given. This being the case it would follow that a very

large proportion of the total number of individuals constituting a

species would diverge considerably from its average condition as regards

each part or organ; and as we know from the previous diagrams of

variation (Figs. 1 to 7) that each part varies to a considerable extent,

\_independently\_, the materials constantly ready for natural selection to

act upon are abundant in quantity and very varied in kind. Almost any

combination of variations of distinct parts will be available, where

required; and this, as we shall see further on, obviates one of the most

weighty objections which have been urged against the efficiency of

natural selection in producing new species, genera, and higher groups.

[Illustration: FIG. 12.]

\_Variation in the Mammalia.\_

Owing to the generally large size of this class of animals, and the

comparatively small number of naturalists who study them, large series

of specimens are only occasionally examined and compared, and thus the

materials for determining the question of their variability in a state

of nature are comparatively scanty. The fact that our domestic animals

belonging to this group, especially dogs, present extreme varieties not

surpassed even by pigeons and poultry among birds, renders it almost

certain that an equal amount of variability exists in the wild state;

and this is confirmed by the example of a species of squirrel (Sciurus

carolinensis), of which sixteen specimens, all males and all taken in

Florida, were measured and tabulated by Mr. Allen. The diagram here

given shows, that, both the general amount of the variation and the

independent variability of the several members of the body, accord

completely with the variations so common in the class of birds; while

their amount and their independence of each other are even greater than

usual.

\_Variation in the Internal Organs of Animals.\_

In case it should be objected that the cases of variation hitherto

adduced are in the external parts only, and that there is no proof that

the internal organs vary in the same manner, it will be advisable to

show that such varieties also occur. It is, however, impossible to

adduce the same amount of evidence in this class of variation, because

the great labour of dissecting large numbers of specimens of the same

species is rarely undertaken, and we have to trust to the chance

observations of anatomists recorded in their regular course of study.

It must, however, be noted that a very large proportion of the

variations already recorded in the external parts of animals necessarily

imply corresponding internal variations. When feet and legs vary in

size, it is because the bones vary; when the head, body, limbs, and tail

change their proportions, the bony skeleton must also change; and even

when the wing or tail feathers of birds become longer or more numerous,

there is sure to be a corresponding change in the bones which support

and the muscles which move them. I will, however, give a few cases of

variations which have been directly observed.

[Illustration: FIG. 13.--Sciurus carolinensis. 32 specimens. Florida.]

Mr. Frank E. Beddard has kindly communicated to me some remarkable

variations he has observed in the internal organs of a species of

earthworm (Perionyx excavatus). The normal characters of this species

are--

Setae forming a complete row round each segment.

Two pairs of spermathecae--spherical pouches without

diverticulae--in segments 8 and 9.

Two pairs of testes in segments 11 and 12.

Ovaries, a single pair in segment 13.

Oviducts open by a common pore in the middle of segment 14.

Vasa deferentia open separately in segment 18, each furnished at

its termination with a large prostate gland.

Between two and three hundred specimens were examined, and among them

thirteen specimens exhibited the following marked variations:--

(1) The number of the spermathecae varied from two to three or

four pairs, their position also varying.

(2) There were occasionally two pairs of ovaries, each with its

own oviduct; the external apertures of these varied in position,

being upon segments 13 and 14, 14 and 15, or 15 and 16.

Occasionally when there was only the normal single oviduct pore

present it varied in position, once occurring on the 10th, and

once on the 11th segment.

(3) The male generative pores varied in position from segments

14 to 20. In one instance there were two pairs instead of the

normal single pair, and in this case each of the four apertures

had its own prostate gland.

Mr. Beddard remarks that all, or nearly all, the above variations are

found \_normally\_ in other genera and species.

When we consider the enormous number of earthworms and the comparatively

very small number of individuals examined, we may be sure, not only that

such variations as these occur with considerable frequency, but also

that still more extraordinary deviations from the normal structure may

often exist.

The next example is taken from Mr. Darwin's unpublished MSS.

"In some species of Shrews (Sorex) and in some field-mice

(Arvicola), the Rev. L. Jenyns (\_Ann. Nat. Hist.\_, vol. vii. pp.

267, 272) found the proportional length of the intestinal canal

to vary considerably. He found the same variability in the

number of the caudal vertebrae. In three specimens of an

Arvicola he found the gall-bladder having a very different

degree of development, and there is reason to believe it is

sometimes absent. Professor Owen has shown that this is the case

with the gall-bladder of the giraffe."

Dr. Crisp (\_Proc. Zool. Soc.\_, 1862, p. 137) found the gall-bladder

present in some specimens of Cervus superciliaris while absent in

others; and he found it to be absent in three giraffes which he

dissected. A double gall-bladder was found in a sheep, and in a small

mammal preserved in the Hunterian Museum there are three distinct

gall-bladders.

The length of the alimentary canal varies greatly. In three adult

giraffes described by Professor Owen it was from 124 to 136 feet long;

one dissected in France had this canal 211 feet long; while Dr. Crisp

measured one of the extraordinary length of 254 feet, and similar

variations are recorded in other animals.[22]

The number of ribs varies in many animals. Mr. St. George Mivart says:

"In the highest forms of the Primates, the number of true ribs is seven,

but in Hylobates there are sometimes eight pairs. In Semnopithecus and

Colobus there are generally seven, but sometimes eight pairs of true

ribs. In the Cebidae there are generally seven or eight pairs, but in

Ateles sometimes nine" (\_Proc. Zool. Soc.\_, 1865, p. 568). In the same

paper it is stated that the number of dorsal vertebrae in man is

normally twelve, very rarely thirteen. In the Chimpanzee there are

normally thirteen dorsal vertebrae, but occasionally there are fourteen

or only twelve.

\_Variations in the Skull.\_

[Illustration: FIG. 14.--Variation of Skull of Wolf. 10 specimens.]

Among the nine adult male Orang-utans, collected by myself in Borneo,

the skulls differed remarkably in size and proportions. The orbits

varied in width and height, the cranial ridge was either single or

double, either much or little developed, and the zygomatic aperture

varied considerably in size. I noted particularly that these

variations bore no necessary relation to each other, so that a large

temporal muscle and zygomatic aperture might exist either with a large

or a small cranium; and thus was explained the curious difference

between the single-crested and the double-crested skulls, which had been

supposed to characterise distinct species. As an instance of the amount

of variation in the skulls of fully adult male orangs, I found the width

between the orbits externally to be only 4 inches in one specimen and

fully 5 inches in another.

Exact measurements of large series of comparable skulls of the mammalia

are not easily found, but from those available I have prepared three

diagrams (Figs. 14, 15, and 16), in order to exhibit the facts of

variation in this very important organ. The first shows the variation in

ten specimens of the common wolf (Canis lupus) from one district in

North America, and we see that it is not only large in amount, but that

each part exhibits a considerable independent variability.[23]

In Diagram 15 we have the variations of eight skulls of the Indian

Honey-bear (Ursus labiatus), as tabulated by the late Dr. J.E. Gray of

the British Museum. For such a small number of specimens the amount of

variation is very large--from one-eighth to one-fifth of the mean

size,--while there are an extraordinary number of instances of

independent variability. In Diagram 16 we have the length and width of

twelve skulls of adult males of the Indian wild boar (Sus cristatus),

also given by Dr. Gray, exhibiting in both sets of measurements a

variation of more than one-sixth, combined with a very considerable

amount of independent variability.[24]

[Illustration: FIG. 15.--Variation of 8 skulls (Ursus labiatus).]

[Illustration: FIG. 16.]

The few facts now given, as to variations of the internal parts of

animals, might be multiplied indefinitely by a search through the

voluminous writings of comparative anatomists. But the evidence already

adduced, taken in conjunction with the much fuller evidence of variation

in all external organs, leads us to the conclusion that wherever

variations are looked for among a considerable number of individuals of

the more common species they are sure to be found; that they are

everywhere of considerable amount, often reaching 20 per cent of the

size of the part implicated; and that they are to a great extent

independent of each other, and thus afford almost any combination of

variations that may be needed.

It must be particularly noticed that the whole series of

variation-diagrams here given (except the three which illustrate the

number of varying individuals) in every case represent the actual amount

of the variation, not on any reduced or enlarged scale, but as it were

life-size. Whatever number of inches or decimals of an inch the species

varies in any of its parts is marked on the diagrams, so that with the

help of an ordinary divided rule or a pair of compasses the variation of

the different parts can be ascertained and compared just as if the

specimens themselves were before the reader, but with much greater ease.

In my lectures on the Darwinian theory in America and in this country I

used diagrams constructed on a different plan, equally illustrating the

large amount of independent variability, but less simple and less

intelligible. The present method is a modification of that used by Mr.

Francis Galton in his researches on the theory of variability, the upper

line (showing the variability of the body) in Diagrams 4, 5, 6, and 13,

being laid down on the method he has used in his experiments with

sweet-peas and in pedigree moth-breeding.[25] I believe, after much

consideration, and many tedious experiments in diagram-making, that no

better method can be adopted for bringing before the eye, both the

amount and the peculiar features of individual variability.

\_Variations of the Habits of Animals.\_

Closely connected with those variations of internal and external

structure which have been already described, are the changes of habits

which often occur in certain individuals or in whole species, since

these must necessarily depend upon some corresponding change in the

brain or in other parts of the organism; and as these changes are of

great importance in relation to the theory of instinct, a few examples

of them will be now adduced.

The Kea (Nestor notabilis) is a curious parrot inhabiting the mountain

ranges of the Middle Island of New Zealand. It belongs to the family of

Brush-tongued parrots, and naturally feeds on the honey of flowers and

the insects which frequent them, together with such fruits or berries as

are found in the region. Till quite recently this comprised its whole

diet, but since the country it inhabits has become occupied by Europeans

it has developed a taste for a carnivorous diet, with alarming results.

It began by picking the sheepskins hung out to dry or the meat in

process of being cured. About 1868 it was first observed to attack

living sheep, which had frequently been found with raw and bleeding

wounds on their backs. Since then it is stated that the bird actually

burrows into the living sheep, eating its way down to the kidneys, which

form its special delicacy. As a natural consequence, the bird is being

destroyed as rapidly as possible, and one of the rare and curious

members of the New Zealand fauna will no doubt shortly cease to exist.

The case affords a remarkable instance of how the climbing feet and

powerful hooked beak developed for one set of purposes can be applied to

another altogether different purpose, and it also shows how little real

stability there may be in what appear to us the most fixed habits of

life. A somewhat similar change of diet has been recorded by the Duke of

Argyll, in which a goose, reared by a golden eagle, was taught by its

foster-parent to eat flesh, which it continued to do regularly and

apparently with great relish.[26]

Change of habits appears to be often a result of imitation, of which Mr.

Tegetmeier gives some good examples. He states that if pigeons are

reared exclusively with small grain, as wheat or barley, they will

starve before eating beans. But when they are thus starving, if a

bean-eating pigeon is put among them, they follow its example, and

thereafter adopt the habit. So fowls sometimes refuse to eat maize, but

on seeing others eat it, they do the same and become excessively fond of

it. Many persons have found that their yellow crocuses were eaten by

sparrows, while the blue, purple, and white coloured varieties were left

untouched; but Mr. Tegetmeier, who grows only these latter colours,

found that after two years the sparrows began to attack them, and

thereafter destroyed them quite as readily as the yellow ones; and he

believes it was merely because some bolder sparrow than the rest set the

example. On this subject Mr. Charles C. Abbott well remarks: "In

studying the habits of our American birds--and I suppose it is true of

birds everywhere--it must at all times be remembered that there is less

stability in the habits of birds than is usually supposed; and no

account of the habits of any one species will exactly detail the various

features of its habits as they really are, in every portion of the

territory it inhabits."[27]

Mr. Charles Dixon has recorded a remarkable change in the mode of

nest-building of some common chaffinches which were taken to New Zealand

and turned out there. He says: "The cup of the nest is small, loosely

put together, apparently lined with feathers, and the walls of the

structure are prolonged for about 18 inches, and hang loosely down the

side of the supporting branch. The whole structure bears some

resemblance to the nests of the hangnests (Icteridae), with the

exception that the cavity is at the top. Clearly these New Zealand

chaffinches were at a loss for a design when fabricating their nest.

They had no standard to work by, no nests of their own kind to copy, no

older birds to give them any instruction, and the result is the abnormal

structure I have just described."[28]

These few examples are sufficient to show that both the habits and

instincts of animals are subject to variation; and had we a sufficient

number of detailed observations we should probably find that these

variations were as numerous, as diverse in character, as large in

amount, and as independent of each other as those which we have seen to

characterise their bodily structure.

\_The Variability of Plants.\_

The variability of plants is notorious, being proved not only by the

endless variations which occur whenever a species is largely grown by

horticulturists, but also by the great difficulty that is felt by

botanists in determining the limits of species in many large genera. As

examples we may take the roses, the brambles, and the willows as well

illustrating this fact. In Mr. Baker's \_Revision of the British Roses\_

(published by the Linnean Society in 1863), he includes under the single

species, Rosa canina--the common dog-rose--no less than twenty-eight

named \_varieties\_ distinguished by more or less constant characters and

often confined to special localities, and to these are referred about

seventy of the \_species\_ of British and continental botanists. Of the

genus Rubus or bramble, \_five\_ British species are given in Bentham's

\_Handbook of the British Flora\_, while in the fifth edition of

Babington's \_Manual of British Botany\_, published about the same time,

no less than \_forty-five\_ species are described. Of willows (Salix) the

same two works enumerate \_fifteen\_ and \_thirty-one\_ species

respectively. The hawkweeds (Hieracium) are equally puzzling, for while

Mr. Bentham admits only seven British species, Professor Babington

describes no less than thirty-two, besides several named varieties.

A French botanist, Mons. A. Jordan, has collected numerous forms of a

common little plant, the spring whitlow-grass (Draba verna); he has

cultivated these for several successive years, and declares that they

preserve their peculiarities unchanged; he also says that they each come

true from seed, and thus possess all the characteristics of true

species. He has described no less than fifty-two such species or

permanent varieties, all found in the south of France; and he urges

botanists to follow his example in collecting, describing, and

cultivating all such varieties as may occur in their respective

districts. Now, as the plant is very common almost all over Europe and

ranges from North America to the Himalayas, the number of similar forms

over this wide area would probably have to be reckoned by hundreds if

not by thousands.

The class of facts now adduced must certainly be held to prove that in

many large genera and in some single species there is a very large

amount of variation, which renders it quite impossible for experts to

agree upon the limits of species. We will now adduce a few striking

cases of individual variation.

The distinguished botanist, Alp. de Candolle, made a special study of

the oaks of the whole world, and has stated some remarkable facts as to

their variability. He declares that on the same branch of oak he has

noted the following variations: (1) In the length of the petiole, as one

to three; (2) in the form of the leaf, being either elliptical or

obovoid; (3) in the margin being entire, or notched, or even pinnatifid;

(4) in the extremity being acute or blunt; (5) in the base being sharp,

blunt, or cordate; (6) in the surface being pubescent or smooth; (7) the

perianth varies in depth and lobing; (8) the stamens vary in number,

independently; (9) the anthers are mucronate or blunt; (10) the fruit

stalks vary greatly in length, often as one to three; (11) the number of

fruits varies; (12) the form of the base of the cup varies; (13) the

scales of the cup vary in form; (14) the proportions of the acorns vary;

(15) the times of the acorns ripening and falling vary.

Besides this, many species exhibit well-marked varieties which have been

described and named, and these are most numerous in the best-known

species. Our British oak (Quercus robur) has twenty-eight varieties;

Quercus Lusitanica has eleven; Quercus calliprinos has ten; and Quercus

coccifera eight.

A most remarkable case of variation in the parts of a common flower has

been given by Dr. Hermann MÃ¼ller. He examined two hundred flowers of

Myosurus minimus, among which he found \_thirty-five\_ different

proportions of the sepals, petals, and anthers, the first varying from

four to seven, the second from two to five, and the third from two to

ten. Five sepals occurred in one hundred and eighty-nine out of the two

hundred, but of these one hundred and five had three petals, forty-six

had four petals, and twenty-six had five petals; but in each of these

sets the anthers varied in number from three to eight, or from two to

nine. We have here an example of the same amount of "independent

variability" that, as we have seen, occurs in the various dimensions of

birds and mammals; and it may be taken as an illustration of the kind

and degree of variability that may be expected to occur among small and

little specialised flowers.[29]

In the common wind-flower (Anemone nemorosa) an almost equal amount of

variation occurs; and I have myself gathered in one locality flowers

varying from 7/8 inch to 1-3/4 inch in diameter; the bracts varying from

1-1/2 inch to 4 inches across; and the petaloid sepals either broad or

narrow, and varying in number from five to ten. Though generally pure

white on their upper surface, some specimens are a full pink, while

others have a decided bluish tinge.

Mr. Darwin states that he carefully examined a large number of plants of

Geranium phaeum and G. pyrenaicum (not perhaps truly British but

frequently found wild), which had escaped from cultivation, and had

spread by seed in an open plantation; and he declares that "the

seedlings varied in almost every single character, both in their flowers

and foliage, to a degree which I have never seen exceeded; yet they

could not have been exposed to any great change of their

conditions."[30]

The following examples of variation in important parts of plants were

collected by Mr. Darwin and have been copied from his unpublished

MSS.:--

"De Candolle (\_Mem. Soc. Phys. de GenÃ¨ve\_, tom. ii. part ii. p. 217)

states that Papaver bracteatum and P. orientale present indifferently

two sepals and four petals, or three sepals and six petals, which is

sufficiently rare with other species of the genus."

"In the Primulacae and in the great class to which this family belongs

the unilocular ovarium is free, but M. Dubury (\_Mem. Soc. Phys. de

GenÃ¨ve\_, tom. ii. p. 406) has often found individuals in Cyclamen

hederaefolium, in which the base of the ovary was connected for a third

part of its length with the inferior part of the calyx."

"M. Aug. St. Hilaire (Sur la Gynobase, \_Mem. des Mus. d'Hist. Nat.\_,

tom. x. p. 134), speaking of some bushes of the Gomphia oleaefolia,

which he at first thought formed a quite distinct species, says: 'VoilÃ

donc dans un mÃªme individu des loges et un style qui se rattachent

tantÃ´t a un axe vertical, et tantÃ´t a un gynobase; donc celui-ci n'est

qu'un axe veritable; mais cet axe est deprimÃ© au lieu d'Ãªtre vertical."

He adds (p. 151), 'Does not all this indicate that nature has tried, in

a manner, in the family of Rutaceae to produce from a single

multilocular ovary, one-styled and symmetrical, several unilocular

ovaries, each with its own style.' And he subsequently shows that, in

Xanthoxylum monogynum, 'it often happens that on the same plant, on the

same panicle, we find flowers with one or with two ovaries;' and that

this is an important character is shown by the Rutaceae (to which

Xanthoxylum belongs), being placed in a group of natural orders

characterised by having a solitary ovary."

"De Candolle has divided the Cruciferae into five sub-orders in

accordance with the position of the radicle and cotyledons, yet Mons. T.

Gay (\_Ann. des Scien. Nat.\_, ser. i. tom. vii. p. 389) found in sixteen

seeds of Petrocallis Pyrenaica the form of the embryo so uncertain that

he could not tell whether it ought to be placed in the sub-orders

'PleurorhizÃ©e' or 'Notor-hizÃ©e'; so again (p. 400) in Cochlearia

saxatilis M. Gay examined twenty-nine embryos, and of these sixteen were

vigorously 'pleurorhizÃ©es,' nine had characters intermediate between

pleuro-and notor-hizÃ©es, and four were pure notor-hizÃ©es."

"M. Raspail asserts (\_Ann. des Scien. Nat.\_, ser. i. tom. v. p. 440)

that a grass (Nostus Borbonicus) is so eminently variable in its floral

organisation, that the varieties might serve to make a family with

sufficiently numerous genera and tribes--a remark which shows that

important organs must be here variable."

\_Species which vary little.\_

The preceding statements, as to the great amount of variation occurring

in animals and plants, do not prove that all species vary to the same

extent, or even vary at all, but, merely, that a considerable number of

species in every class, order, and family do so vary. It will have been

observed that the examples of great variability have all been taken from

common species, or species which have a wide range and are abundant in

individuals. Now Mr. Darwin concludes, from an elaborate examination of

the floras and faunas of several distinct regions, that common, wide

ranging species, as a rule, vary most, while those that are confined to

special districts and are therefore comparatively limited in number of

individuals vary least. By a similar comparison it is shown that species

of large genera vary more than species of small genera. These facts

explain, to some extent, why the opinion has been so prevalent that

variation is very limited in amount and exceptional in character. For

naturalists of the old school, and all mere collectors, were interested

in species in proportion to their rarity, and would often have in their

collections a larger number of specimens of a rare species than of a

species that was very common. Now as these rare species do really vary

much less than the common species, and in many cases hardly vary at all,

it was very natural that a belief in the fixity of species should

prevail. It is not, however, as we shall see presently, the rare, but

the common and widespread species which become the parents of new forms,

and thus the non-variability of any number of rare or local species

offers no difficulty whatever in the way of the theory of evolution.

\_Concluding Remarks.\_

We have now shown in some detail, at the risk of being tedious, that

individual variability is a general character of all common and

widespread species of animals or plants; and, further, that this

variability extends, so far as we know, to every part and organ, whether

external or internal, as well as to every mental faculty. Yet more

important is the fact that each part or organ varies to a considerable

extent independently of other parts. Again, we have shown, by abundant

evidence, that the variation that occurs is very large in

amount--usually reaching 10 or 20, and sometimes even 25 per cent of the

average size of the varying part; while not one or two only, but from 5

to 10 per cent of the specimens examined exhibit nearly as large an

amount of variation. These facts have been brought clearly before the

reader by means of numerous diagrams, drawn to scale and exhibiting the

actual variations in inches, so that there can be no possibility of

denying either their generality or their amount. The importance of this

full exposition of the subject will be seen in future chapters, when we

shall frequently have to refer to the facts here set forth, especially

when we deal with the various theories of recent writers and the

criticisms that have been made of the Darwinian theory.

A full exposition of the facts of variation among wild animals and

plants is the more necessary, because comparatively few of them were

published in Mr. Darwin's works, while the more important have only been

made known since the last edition of \_The Origin of Species\_ was

prepared; and it is clear that Mr. Darwin himself did not fully

recognise the enormous amount of variability that actually exists. This

is indicated by his frequent reference to the extreme slowness of the

changes for which variation furnishes the materials, and also by his use

of such expressions as the following: "A variety when once formed must

again, \_perhaps after a long interval of time\_, vary or present

individual differences of the same favourable nature as before"

(\_Origin\_, p. 66). And again, after speaking of changed conditions

"affording a better chance of the occurrence of favourable variations,"

he adds: "\_Unless such occur natural selection can do nothing\_"

(\_Origin\_, p. 64). These expressions are hardly consistent with the fact

of the constant and large amount of variation, of every part, in all

directions, which evidently occurs in each generation of all the more

abundant species, and which must afford an ample supply of favourable

variations whenever required; and they have been seized upon and

exaggerated by some writers as proofs of the extreme difficulties in the

way of the theory. It is to show that such difficulties do not exist,

and in the full conviction that an adequate knowledge of the facts of

variation affords the only sure foundation for the Darwinian theory of

the origin of species, that this chapter has been written.

FOOTNOTES:

[Footnote 16: \_Foraminifera\_, preface, p. x.]

[Footnote 17: \_United States Geological Survey of the Territories\_,

1874.]

[Footnote 18: \_Proceedings of the Entomological Society of London\_,

1875, p. vii.]

[Footnote 19: \_Ann. des Sci. Nat.\_, tom. xvi. p. 50.]

[Footnote 20: See \_Winter Birds of Florida\_, p. 206, Table F.]

[Footnote 21: See Table I, p. 211, of Allen's \_Winter Birds of

Florida\_.]

[Footnote 22: \_Proc. Zool. Soc.\_, 1864, p. 64.]

[Footnote 23: J.A. Allen, on Geographical Variation among North American

Mammals, \_Bull. U.S. Geol. and Geog. Survey\_, vol. ii. p. 314 (1876).]

[Footnote 24: \_Proc. Zool. Soc. Lond.\_, 1864, p. 700, and 1868, p. 28.]

[Footnote 25: See \_Trans. Entomological Society of London\_, 1887, p.

24.]

[Footnote 26: \_Nature\_, vol. xix. p. 554.]

[Footnote 27: \_Nature\_, vol. xvi. p. 163; and vol. xi. p. 227.]

[Footnote 28: \_Ibid.\_, vol. xxxi. (1885), p. 533.]

[Footnote 29: \_Nature\_, vol. xxvi. p. 81.]

[Footnote 30: \_Animals and Plants under Domestication\_, vol. ii. p.

258.]

CHAPTER IV

VARIATION OF DOMESTICATED ANIMALS AND CULTIVATED PLANTS

The facts of variation and artificial selection--Proofs of the

generality of variation--Variations of apples and

melons--Variations of flowers--Variations of domestic

animals--Domestic pigeons--Acclimatisation--Circumstances

favourable to selection by man--Conditions favourable to

variation--Concluding remarks.

Having so fully discussed variation under nature it will be unnecessary

to devote so much space to domesticated animals and cultivated plants,

especially as Mr. Darwin has published two remarkable volumes on the

subject where those who desire it may obtain ample information. A

general sketch of the more important facts will, however, be given, for

the purpose of showing how closely they correspond with those described

in the preceding chapter, and also to point out the general principles

which they illustrate. It will also be necessary to explain how these

variations have been increased and accumulated by artificial selection,

since we are thereby better enabled to understand the action of natural

selection, to be discussed in the succeeding chapter.

\_The facts of Variation and Artificial Selection.\_

Every one knows that in each litter of kittens or of puppies no two are

alike. Even in the case in which several are exactly alike in colours,

other differences are always perceptible to those who observe them

closely. They will differ in size, in the proportions of their bodies

and limbs, in the length or texture of their hairy covering, and notably

in their disposition. They each possess, too, an individual

countenance, almost as varied when closely studied as that of a human

being; not only can a shepherd distinguish every sheep in his flock, but

we all know that each kitten in the successive families of our old

favourite cat has a face of its own, with an expression and

individuality distinct from all its brothers and sisters. Now this

individual variability exists among all creatures whatever, which we can

closely observe, even when the two parents are very much alike and have

been matched in order to preserve some special breed. The same thing

occurs in the vegetable kingdom. All plants raised from seed differ more

or less from each other. In every bed of flowers or of vegetables we

shall find, if we look closely, that there are countless small

differences, in the size, in the mode of growth, in the shape or colour

of the leaves, in the form, colour, or markings of the flowers, or in

the size, form, colour, or flavour of the fruit. These differences are

usually small, but are yet easily seen, and in their extremes are very

considerable; and they have this important quality, that they have a

tendency to be reproduced, and thus by careful breeding any particular

variation or group of variations can be increased to an enormous

extent--apparently to any extent not incompatible with the life, growth,

and reproduction of the plant or animal.

The way this is done is by artificial selection, and it is very

important to understand this process and its results. Suppose we have a

plant with a small edible seed, and we want to increase the size of that

seed. We grow as large a quantity of it as possible, and when the crop

is ripe we carefully choose a few of the very largest seeds, or we may

by means of a sieve sort out a quantity of the largest seeds. Next year

we sow only these large seeds, taking care to give them suitable soil

and manure, and the result is found to be that the \_average\_ size of the

seeds is larger than in the first crop, and that the largest seeds are

now somewhat larger and more numerous. Again sowing these, we obtain a

further slight increase of size, and in a very few years we obtain a

greatly improved race, which will always produce larger seeds than the

unimproved race, even if cultivated without any special care. In this

way all our fine sorts of vegetables, fruits, and flowers have been

obtained, all our choice breeds of cattle or of poultry, our wonderful

race-horses, and our endless varieties of dogs. It is a very common but

mistaken idea that this improvement is due to crossing and feeding in

the case of animals, and to improved cultivation in the case of plants.

Crossing is occasionally used in order to obtain a combination of

qualities found in two distinct breeds, and also because it is found to

increase the constitutional vigour; but every breed possessing any

exceptional quality is the result of the selection of variations

occurring year after year and accumulated in the manner just described.

Purity of breed, with repeated selection of the best varieties of that

breed, is the foundation of all improvement in our domestic animals and

cultivated plants.

\_Proofs of the Generality of Variation.\_

Another very common error is, that variation is the exception, and

rather a rare exception, and that it occurs only in one direction at a

time--that is, that only one or two of the numerous possible modes of

variation occur at the same time. The experience of breeders and

cultivators, however, proves that variation is the rule instead of the

exception, and that it occurs, more or less, in almost every direction.

This is shown by the fact that different species of plants and animals

have required different \_kinds\_ of modification to adapt them to our

use, and we have never failed to meet with variation \_in that particular

direction\_, so as to enable us to accumulate it and so to produce

ultimately a large amount of change in the required direction. Our

gardens furnish us with numberless examples of this property of plants.

In the cabbage and lettuce we have found variation in the size and mode

of growth of the leaf, enabling us to produce by selection the almost

innumerable varieties, some with solid heads of foliage quite unlike any

plant in a state of nature, others with curiously wrinkled leaves like

the savoy, others of a deep purple colour used for pickling. From the

very same species as the cabbage (Brassica oleracea) have arisen the

broccoli and cauliflower, in which the leaves have undergone little

alteration, while the branching heads of flowers grow into a compact

mass forming one of our most delicate vegetables. The brussels sprouts

are another form of the same plant, in which the whole mode of growth

has been altered, numerous little heads of leaves being produced on the

stem. In other varieties the ribs of the leaves are thickened so as to

become themselves a culinary vegetable; while, in the Kohlrabi, the stem

grows into a turnip-like mass just above ground. Now all these

extraordinarily distinct plants come from one original species which

still grows wild on our coasts; and it must have varied in all these

directions, otherwise variations could not have been accumulated to the

extent we now see them. The flowers and seeds of all these plants have

remained nearly stationary, because no attempt has been made to

accumulate the slight variations that no doubt occur in them.

If now we turn to another set of plants, the turnips, radishes, carrots,

and potatoes, we find that the roots or underground tubers have been

wonderfully enlarged and improved, and also altered in shape and colour,

while the stems, leaves, flowers, and fruits have remained almost

unchanged. In the various kinds of peas and beans it is the pod or fruit

and the seed that has been subjected to selection, and therefore greatly

modified; and it is here very important to notice that while all these

plants have undergone cultivation in a great variety of soils and

climates, with different manures and under different systems, yet the

flowers have remained but little altered, those of the broad bean, the

scarlet-runner, and the garden-pea, being nearly the same in all the

varieties. This shows us how little change is produced by mere

cultivation, or even by variety of soil and climate, if there is no

\_selection\_ to preserve and accumulate the small variations that are

continually occurring. When, however, a great amount of modification has

been effected in one country, change to another country produces a

decided effect. Thus it has been found that some of the numerous

varieties of maize produced and cultivated in the United States change

considerably, not only in their size and colour, but even in the shape

of the seed when grown for a few successive years in Germany.[31] In all

our cultivated fruit trees the fruits vary immensely in shape, size,

colour, flavour, time of ripening, and other qualities, while the leaves

and flowers usually differ so little that they are hardly

distinguishable except to a very close observer.

\_Variations of Apples and of Melons.\_

The most remarkable varieties are afforded by the apple and the melon,

and some account of these will be given as illustrating the effects of

slight variations accumulated by selection. All our apples are known to

have descended from the common crab of our hedges (Pyrus malus), and

from this at least a thousand distinct varieties have been produced.

These differ greatly in the size and form of the fruit, in its colour,

and in the texture of the skin. They further differ in the time of

ripening, in their flavour, and in their keeping properties; but apple

trees also differ in many other ways. The foliage of the different

varieties can often be distinguished by peculiarities of form and

colour, and it varies considerably in the time of its appearance; in

some hardly a leaf appears till the tree is in full bloom, while others

produce their leaves so early as almost to hide the flowers. The flowers

differ in size and colour, and in one case in structure also, that of

the St. Valery apple having a double calyx with ten divisions, and

fourteen styles with oblique stigmas, but without stamens or corolla.

The flowers, therefore, have to be fertilised with the pollen from other

varieties in order to produce fruit. The pips or seeds differ also in

shape, size, and colour; some varieties are liable to canker more than

others, while the Winter Majetin and one or two others have the strange

constitutional peculiarity of never being attacked by the mealy bug even

when all the other trees in the same orchard are infested with it.

All the cucumbers and gourds vary immensely, but the melon (Cucumis

melo) exceeds them all. A French botanist, M. Naudin, devoted six years

to their study. He found that previous botanists had described thirty

distinct species, as they thought, which were really only varieties of

melons. They differ chiefly in their fruits, but also very much in

foliage and mode of growth. Some melons are only as large as small

plums, others weigh as much as sixty-six pounds. One variety has a

scarlet fruit. Another is not more than an inch in diameter, but

sometimes more than a yard in length, twisting about in all directions

like a serpent. Some melons are exactly like cucumbers; and an Algerian

variety, when ripe, cracks and falls to pieces, just as occurs in a

wild gourd (C. momordica).[32]

\_Variations of Flowers.\_

Turning to flowers, we find that in the same genus as our currant and

gooseberry, which we have cultivated for their fruits, there are some

ornamental species, as the Ribes sanguinea, and in these the flowers

have been selected so as to produce deep red, pink, or white varieties.

When any particular flower becomes fashionable and is grown in large

quantities, variations are always met with sufficient to produce great

varieties of tint or marking, as shown by our roses, auriculas, and

geraniums. When varied leaves are required, it is found that a number of

plants vary sufficiently in this direction also, and we have zonal

geraniums, variegated ivies, gold and silver marked hollies, and many

others.

\_Variations of Domestic Animals.\_

Coming now to our domesticated animals, we find still more extraordinary

cases; and it appears as if any special quality or modification in an

animal can be obtained if we only breed it in sufficient quantity, watch

carefully for the required variations, and carry on selection with

patience and skill for a sufficiently long period. Thus, in sheep we

have enormously increased the wool, and have obtained the power of

rapidly forming flesh and fat; in cows we have increased the production

of milk; in horses we have obtained strength, endurance, or speed, and

have greatly modified size, form, and colour; in poultry we have secured

various colours of plumage, increase of size, and almost perpetual

egg-laying. But it is in dogs and pigeons that the most marvellous

changes have been effected, and these require our special attention.

Our various domestic dogs are believed to have originated from several

distinct wild species, because in every part of the world the native

dogs resemble some wild dogs or wolves of the same country. Thus perhaps

several species of wolves and jackals were domesticated in very early

times, and from breeds derived from these, crossed and improved by

selection, our existing dogs have descended. But this intermixture of

distinct species will go a very little way in accounting for the

peculiarities of the different breeds of dogs, many of which are totally

unlike any wild animal. Such is the case with greyhounds, bloodhounds,

bulldogs, Blenheim spaniels, terriers, pugs, turnspits, pointers, and

many others; and these differ so greatly in size, shape, colour, and

habits, as well as in the form and proportions of all the different

parts of the body, that it seems impossible that they could have

descended from any of the known wild dogs, wolves, or allied animals,

none of which differ nearly so much in size, form, and proportions. We

have here a remarkable proof that variation is not confined to

superficial characters--to the colour, hair, or external appendages,

when we see how the entire skeletons of such forms as the greyhound and

the bulldog have been gradually changed in opposite directions till they

are both completely unlike that of any known wild animal, recent or

extinct. These changes have been the result of some thousands of years

of domestication and selection, different breeds being used and

preserved for different purposes; but some of the best breeds are known

to have been improved and perfected in modern times. About the middle of

the last century a new and improved kind of foxhound was produced; the

greyhound was also greatly improved at the end of the last century,

while the true bulldog was brought to perfection about the same period.

The Newfoundland dog has been so much changed since it was first

imported that it is now quite unlike any existing native dog in that

island.[33]

\_Domestic Pigeons.\_

The most remarkable and instructive example of variation produced by

human selection is afforded by the various races and breeds of domestic

pigeons, not only because the variations produced are often most

extraordinary in amount and diverse in character, but because in this

case there is no doubt whatever that all have been derived from one wild

species, the common rock-pigeon (Columba livia). As this is a very

important point it is well to state the evidence on which the belief is

founded. The wild rock-pigeon is of a slaty-blue colour, the tail has a

dark band across the end, the wings have two black bands, and the outer

tail-feathers are edged with white at the base. No other wild pigeon in

the world has this combination of characters. Now in every one of the

domestic varieties, even the most extreme, all the above marks, even to

the white edging of the outer tail-feathers, are sometimes found

perfectly developed. When birds belonging to two distinct breeds are

crossed one or more times, neither of the parents being blue, or having

any of the above-named marks, the mongrel offspring are very apt to

acquire some of these characters. Mr. Darwin gives instances which he

observed himself. He crossed some white fantails with some black barbs,

and the mongrels were black, brown, or mottled. He also crossed a barb

with a spot, which is a white bird with a red tail and red spot on the

forehead, and the mongrel offspring were dusky and mottled. On now

crossing these two sets of mongrels with each other, he obtained a bird

of a beautiful blue colour, with the barred and white edged tail, and

double-banded wings, so as almost exactly to resemble a wild

rock-pigeon. This bird was descended in the second generation from a

pure white and pure black bird, both of which when unmixed breed their

kind remarkably true. These facts, well known to experienced

pigeon-fanciers, together with the habits of the birds, which all like

to nest in holes, or dovecots, not in trees like the great majority of

wild pigeons, have led to the general belief in the single origin of all

the different kinds.

In order to afford some idea of the great differences which exist among

domesticated pigeons, it will be well to give a brief abstract of Mr.

Darwin's account of them. He divides them into eleven distinct races,

most of which have several sub-races.

RACE I. \_Pouters\_.--These are especially distinguished by the enormously

enlarged crop, which can be so inflated in some birds as almost to

conceal the beak. They are very long in the body and legs and stand

almost upright, so as to present a very distinct appearance. Their

skeleton has become modified, the ribs being broader and the vertebrae

more numerous than in other pigeons.

RACE II. \_Carriers\_.--These are large, long-necked birds, with a long

pointed beak, and the eyes surrounded with a naked carunculated skin or

wattle, which is also largely developed at the base of the beak. The

opening of the mouth is unusually wide. There are several sub-races, one

being called Dragons.

RACE III. \_Runts\_.--These are very large-bodied, long-beaked pigeons,

with naked skin round the eyes. The wings are usually very long, the

legs long, and the feet large, and the skin of the neck is often red.

There are several sub-races, and these differ very much, forming a

series of links between the wild rock-pigeon and the carrier.

RACE IV. \_Barbs\_.--These are remarkable for their very short and thick

beak, so unlike that of most pigeons that fanciers compare it with that

of a bullfinch. They have also a naked carunculated skin round the eyes,

and the skin over the nostrils swollen.

RACE V. \_Fantails\_.--Short-bodied and rather small-beaked pigeons, with

an enormously developed tail, consisting usually of from fourteen to

forty feathers instead of twelve, the regular number in all other

pigeons, wild and tame. The tail spreads out like a fan and is usually

carried erect, and the bird bends back its slender neck, so that in

highly-bred varieties the head touches the tail. The feet are small, and

they walk stiffly.

RACE VI. \_Turbits and Owls\_.--These are characterised by the feathers of

the middle of neck and breast in front spreading out irregularly so as

to form a frill. The Turbits also have a crest on the head, and both

have the beak exceedingly short.

RACE VII. \_Tumblers\_.--- These have a small body and short beak, but

they are specially distinguished by the singular habit of tumbling over

backwards during flight. One of the sub-races, the Indian Lotan or

Ground tumbler, if slightly shaken and placed on the ground, will

immediately begin tumbling head over heels until taken up and soothed.

If not taken up, some of them will go on tumbling till they die. Some

English tumblers are almost equally persistent. A writer, quoted by Mr.

Darwin, says that these birds generally begin to tumble almost as soon

as they can fly; "at three months old they tumble well, but still fly

strong; at five or six months they tumble excessively; and in the second

year they mostly give up flying, on account of their tumbling so much

and so close to the ground. Some fly round with the flock, throwing a

clean summersault every few yards till they are obliged to settle from

giddiness and exhaustion. These are called Air-tumblers, and they

commonly throw from twenty to thirty summersaults in a minute, each

clear and clean. I have one red cock that I have on two or three

occasions timed by my watch, and counted forty summersaults in the

minute. At first they throw a single summersault, then it is double,

till it becomes a continuous roll, which puts an end to flying, for if

they fly a few yards over they go, and roll till they reach the ground.

Thus I had one kill herself, and another broke his leg. Many of them

turn over only a few inches from the ground, and will tumble two or

three times in flying across their loft. These are called House-tumblers

from tumbling in the house. The act of tumbling seems to be one over

which they have no control, an involuntary movement which they seem to

try to prevent. I have seen a bird sometimes in his struggles fly a yard

or two straight upwards, the impulse forcing him backwards while he

struggles to go forwards."[34]

The Short-faced tumblers are an improved sub-race which have almost lost

the power of tumbling, but are valued for possessing some other

characteristics in an extreme degree. They are very small, have almost

globular heads, and a very minute beak, so that fanciers say the head of

a perfect bird should resemble a cherry with a barleycorn stuck in it.

Some of these weigh less than seven ounces, whereas the wild rock-pigeon

weighs about fourteen ounces. The feet, too, are very short and small,

and the middle toe has twelve or thirteen instead of fourteen or fifteen

scutellae. They have often only nine primary wing-feathers instead of

ten as in all other pigeons.

RACE VIII. \_Indian Frill-back\_.--In these birds the beak is very short,

and the feathers of the whole body are reversed or turn backwards.

RACE IX. \_Jacobin\_.--These curious birds have a hood of feathers almost

enclosing the head and meeting in front of the neck. The wings and tail

are unusually long.

RACE X. \_Trumpeter\_.--Distinguished by a tuft of feathers curling

forwards over the beak, and the feet very much feathered. They obtain

their name from the peculiar voice unlike that of any other pigeon. The

coo is rapidly repeated, and is continued for several minutes. The feet

are covered with feathers so large as often to appear like little wings.

RACE XI. comprises \_Laughers\_, \_Frill-backs\_, \_Nuns\_, \_Spots\_, \_and

Swallows\_.--They are all very like the common rock-pigeon, but have each

some slight peculiarity. The Laughers have a peculiar voice, supposed to

resemble a laugh. The Nuns are white, with the head, tail, and primary

wing-feathers black or red. The Spots are white, with the tail and a

spot on the forehead red. The Swallows are slender, white in colour,

with the head and wings of some darker colour.

Besides these races and sub-races a number of other kinds have been

described, and about one hundred and fifty varieties can be

distinguished. It is interesting to note that almost every part of the

bird, whose variations can be noted and selected, has led to variations

of a considerable extent, and many of these have necessitated changes in

the plumage and in the skeleton quite as great as any that occur in the

numerous distinct species of large genera. The form of the skull and

beak varies enormously, so that the skulls of the Short-faced tumbler

and some of the Carriers differ more than any wild pigeons, even those

classed in distinct genera. The breadth and number of the ribs vary, as

well as the processes on them; the number of the vertebrae and the

length of the sternum also vary; and the perforations in the sternum

vary in size and shape. The oil gland varies in development, and is

sometimes absent. The number of the wing-feathers varies, and those of

the tail to an enormous extent. The proportions of the leg and feet and

the number of the scutellae also vary. The eggs also vary somewhat in

size and shape; and the amount of downy clothing on the young bird, when

first hatched, differs very considerably. Finally, the attitude of the

body, the manner of walking, the mode of flight, and the voice, all

exhibit modifications of the most remarkable kind.[35]

\_Acclimatisation\_.

A very important kind of variation is that constitutional change termed

acclimatisation, which enables any organism to become gradually adapted

to a different climate from the parent stock. As closely allied species

often inhabit different countries possessing very different climates, we

should expect to find cases illustrating this change among our

domesticated animals and cultivated plants. A few examples will

therefore be adduced showing that such constitutional variation does

occur.

Among animals the cases are not numerous, because no systematic attempt

has been made to select varieties for this special quality. It has,

however, been observed that, though no European dogs thrive well in

India, the Newfoundland dog, originating from a severe climate, can

hardly be kept alive. A better case, perhaps, is furnished by merino

sheep, which, when imported directly from England, do not thrive, while

those which have been bred in the intermediate climate of the Cape of

Good Hope do much better. When geese were first introduced into Bogota,

they laid few eggs at long intervals, and few of the young survived. By

degrees, however, the fecundity improved, and in about twenty years

became equal to what it is in Europe. According to Garcilaso, when fowls

were first introduced into Peru they were not fertile, whereas now they

are as much so as in Europe.

Plants furnish much more important evidence. Our nurserymen distinguish

in their catalogues varieties of fruit-trees which are more or less

hardy, and this is especially the case in America, where certain

varieties only will stand the severe climate of Canada. There is one

variety of pear, the Forelle, which both in England and France withstood

frosts that killed the flowers and buds of all other kinds of pears.

Wheat, which is grown over so large a portion of the world, has become

adapted to special climates. Wheat imported from India and sown in good

wheat soil in England produced the most meagre ears; while wheat taken

from France to the West Indian Islands produced either wholly barren

spikes or spikes furnished with two or three miserable seeds, while West

Indian seed by its side yielded an enormous harvest. The orange was very

tender when first introduced into Italy, and continued so as long as it

was propagated by grafts, but when trees were raised from seed many of

these were found to be hardier, and the orange is now perfectly

acclimatised in Italy. Sweet-peas (Lathyrus odoratus) imported from

England to the Calcutta Botanic Gardens produced few blossoms and no

seed; those from France flowered a little better, but still produced no

seed, but plants raised from seed brought from Darjeeling in the

Himalayas, but originally derived from England, flower and seed

profusely in Calcutta.[36]

An observation by Mr. Darwin himself is perhaps even more instructive.

He says: "On 24th May 1864 there was a severe frost in Kent, and two

rows of scarlet runners (Phaseolus multiflorus) in my garden, containing

390 plants of the same age and equally exposed, were all blackened and

killed except about a dozen plants. In an adjoining row of Fulmer's

dwarf bean (Phaseolus vulgaris) one single plant escaped. A still more

severe frost occurred four days afterwards, and of the dozen plants

which had previously escaped only three survived; these were not taller

or more vigorous than the other young plants, but they escaped

completely, with not even the tips of their leaves browned. It was

impossible to behold these three plants, with their blackened, withered,

and dead brethren all around them, and not see at a glance that they

differed widely in their constitutional power of resisting frost."

The preceding sketch of the variation that occurs among domestic animals

and cultivated plants shows how wide it is in range and how great in

amount; and we have good reason to believe that similar variation

extends to all organised beings. In the class of fishes, for example, we

have one kind which has been long domesticated in the East, the gold

and silver carps; and these present great variation, not only of colour

but in the form and structure of the fins and other external organs. In

like manner, the only domesticated insects, hive bees and silkworm

moths, present numbers of remarkable varieties which have been produced

by the selection of chance variations just as in the case of plants and

the higher animals.

\_Circumstances favourable to Selection by Man.\_

It may be supposed, that the systematic selection which has been

employed for the purpose of improving the races of animals or plants

useful to man is of comparatively recent origin, though some of the

different races are known to have been in existence in very early times.

But Mr. Darwin has pointed out, that unconscious selection must have

begun to produce an effect as soon as plants were cultivated or animals

domesticated by man. It would have been very soon observed that animals

and plants produced their like, that seed of early wheat produced early

wheat, that the offspring of very swift dogs were also swift, and as

every one would try to have a good rather than a bad sort this would

necessarily lead to the slow but steady improvement of all useful plants

and animals subject to man's care. Soon there would arise distinct

breeds, owing to the varying uses to which the animals and plants were

put. Dogs would be wanted chiefly to hunt one kind of game in one part

of the country and another kind elsewhere; for one purpose scent would

be more important, for another swiftness, for another strength and

courage, for yet another watchfulness and intelligence, and this would

soon lead to the formation of very distinct races. In the case of

vegetables and fruits, different varieties would be found to succeed

best in certain soils and climates; some might be preferred on account

of the quantity of food they produced, others for their sweetness and

tenderness, while others might be more useful on account of their

ripening at a particular season, and thus again distinct varieties would

be established. An instance of unconscious selection leading to distinct

results in modern times is afforded by two flocks of Leicester sheep

which both originated from the same stock, and were then bred pure for

upwards of fifty years by two gentlemen, Mr. Buckley and Mr. Burgess.

Mr. Youatt, one of the greatest authorities on breeding domestic

animals, says: "There is not a suspicion existing in the mind of any one

at all acquainted with the subject that the owner of either of them has

deviated in any one instance from the pure blood of Mr. Bakewell's

original flock, and yet the difference between the sheep possessed by

these two gentlemen is so great that they have the appearance of being

quite different varieties." In this case there was no desire to deviate

from the original breed, and the difference must have arisen from some

slight difference of taste or judgment in selecting, each year, the

parents for the next year's stock, combined perhaps with some direct

effect of the slight differences of climate and soil on the two farms.

Most of our domesticated animals and cultivated plants have come to us

from the earliest seats of civilisation in Western Asia or Egypt, and

have therefore been the subjects of human care and selection for some

thousands of years, the result being that, in many cases, we do not know

the wild stock from which they originally sprang. The horse, the camel,

and the common bull and cow are nowhere found in a wild state, and they

have all been domesticated from remote antiquity. The original of the

domestic fowl is still wild in India and the Malay Islands, and it was

domesticated in India and China before 1400 B.C. It was introduced into

Europe about 600 B.C. Several distinct breeds were known to the Romans

about the commencement of the Christian era, and they have since spread

all over the civilised world and been subjected to a vast amount of

conscious and unconscious selection, to many varieties of climate and to

differences of food; the result being seen in the wonderful diversity of

breeds which differ quite as remarkably as do the different races of

pigeons already described.

In the vegetable kingdom, most of the cereals--wheat, barley, etc.--are

unknown as truly wild plants; and the same is the case with many

vegetables, for De Candolle states that out of 157 useful cultivated

plants thirty-two are quite unknown in a wild state, and that forty more

are of doubtful origin. It is not improbable that most of these do exist

wild, but they have been so profoundly changed by thousands of years of

cultivation as to be quite unrecognisable. The peach is unknown in a

wild state, unless it is derived from the common almond, on which point

there is much difference of opinion among botanists and horticulturists.

The immense antiquity of most of our cultivated plants sufficiently

explains the apparent absence of such useful productions in Australia

and the Cape of Good Hope, notwithstanding that they both possess an

exceedingly rich and varied flora. These countries having been, until a

comparatively recent period, inhabited only by uncivilised men, neither

cultivation nor selection has been carried on for a sufficiently long

time. In North America, however, where there was evidently a very

ancient if low form of civilisation, as indicated by the remarkable

mounds, earthworks, and other prehistoric remains, maize was cultivated,

though it was probably derived from Peru; and the ancient civilisation

of that country and of Mexico has given rise to no fewer than

thirty-three useful cultivated plants.

\_Conditions favourable to the production of Variations.\_

In order that plants and animals may be improved and modified to any

considerable extent, it is of course essential that suitable variations

should occur with tolerable frequency. There seem to be three conditions

which are especially favourable to the production of variations: (1)

That the particular species or variety should be kept in very large

numbers; (2) that it should be spread over a wide area and thus

subjected to a considerable diversity of physical conditions; and (3)

that it should be occasionally crossed with some distinct but closely

allied race. The first of these conditions is perhaps the most

important, the chance of variations of any particular kind being

increased in proportion to the quantity of the original stock and of its

annual offspring. It has been remarked that only those breeders who keep

large flocks can effect much improvement; and it is for the same reason

that pigeons and fowls, which can be so easily and rapidly increased,

and which have been kept in such large numbers by so great a number of

persons, have produced such strange and numerous varieties. In like

manner, nurserymen who grow fruit and flowers in large quantities have a

great advantage over private amateurs in the production of new

varieties.

Although I believe, for reasons which will be given further on, that

some amount of variability is a constant and necessary property of all

organisms, yet there appears to be good evidence to show that changed

conditions of life tend to increase it, both by a direct action on the

organisation and by indirectly affecting the reproductive system. Hence

the extension of civilisation, by favouring domestication under altered

conditions, facilitates the process of modification. Yet this change

does not seem to be an essential condition, for nowhere has the

production of extreme varieties of plants and flowers been carried

farther than in Japan, where careful selection continued for many

generations must have been the chief factor. The effect of occasional

crosses often results in a great amount of variation, but it also leads

to instability of character, and is therefore very little employed in

the production of fixed and well-marked races. For this purpose, in

fact, it has to be carefully avoided, as it is only by isolation and

pure breeding that any specially desired qualities can be increased by

selection. It is for this reason that among savage peoples, whose

animals run half wild, little improvement takes place; and the

difficulty of isolation also explains why distinct and pure breeds of

cats are so rarely met with. The wide distribution of useful animals and

plants from a very remote epoch has, no doubt, been a powerful cause of

modification, because the particular breed first introduced into each

country has often been kept pure for many years, and has also been

subjected to slight differences of conditions. It will also usually have

been selected for a somewhat different purpose in each locality, and

thus very distinct races would soon originate.

The important physiological effects of crossing breeds or strains, and

the part this plays in the economy of nature, will be explained in a

future chapter.

\_Concluding Remarks.\_

The examples of variation now adduced--and these might have been almost

indefinitely increased--will suffice to show that there is hardly an

organ or a quality in plants or animals which has not been observed to

vary; and further, that whenever any of these variations have been

useful to man he has been able to increase them to a marvellous extent

by the simple process of always preserving the best varieties to breed

from. Along with these larger variations others of smaller amount

occasionally appear, sometimes in external, sometimes in internal

characters, the very bones of the skeleton often changing slightly in

form, size, or number; but as these secondary characters have been of no

use to man, and have not been specially selected by him, they have,

usually, not been developed to any great amount except when they have

been closely dependent on those external characters which he has largely

modified.

As man has considered only utility to himself, or the satisfaction of

his love of beauty, of novelty, or merely of something strange or

amusing, the variations he has thus produced have something of the

character of monstrosities. Not only are they often of no use to the

animals or plants themselves, but they are not unfrequently injurious to

them. In the Tumbler pigeons, for instance, the habit of tumbling is

sometimes so excessive as to injure or kill the bird; and many of our

highly-bred animals have such delicate constitutions that they are very

liable to disease, while their extreme peculiarities of form or

structure would often render them quite unfit to live in a wild state.

In plants, many of our double flowers, and some fruits, have lost the

power of producing seed, and the race can thus be continued only by

means of cuttings or grafts. This peculiar character of domestic

productions distinguishes them broadly from wild species and varieties,

which, as will be seen by and by, are necessarily adapted in every part

of their organisation to the conditions under which they have to live.

Their importance for our present inquiry depends on their demonstrating

the occurrence of incessant slight variations in all parts of an

organism, with the transmission to the offspring of the special

characteristics of the parents; and also, that all such slight

variations are capable of being accumulated by selection till they

present very large and important divergencies from the ancestral stock.

We thus see, that the evidence as to variation afforded by animals and

plants under domestication strikingly accords with that which we have

proved to exist in a state of nature. And it is not at all surprising

that it should be so, since all the species were in a state of nature

when first domesticated or cultivated by man, and whatever variations

occur must be due to purely natural causes. Moreover, on comparing the

variations which occur in any one generation of domesticated animals

with those which we know to occur in wild animals, we find no evidence

of greater individual variation in the former than in the latter. The

results of man's selection are more striking to us because we have

always considered the varieties of each domestic animal to be

essentially identical, while those which we observe in a wild state are

held to be essentially diverse. The greyhound and the spaniel seem

wonderful, as varieties of one animal produced by man's selection; while

we think little of the diversities of the fox and the wolf, or the horse

and the zebra, because we have been accustomed to look upon them as

radically distinct animals, not as the results of nature's selection of

the varieties of a common ancestor.

FOOTNOTES:

[Footnote 31: Darwin, \_Animals and Plants under Domestication\_, vol. i.

p. 322.]

[Footnote 32: These facts are taken from Darwin's \_Domesticated Animals

and Cultivated Plants\_, vol. i. pp. 359, 360, 392-401; vol. ii. pp. 231,

275, 330.]

[Footnote 33: See Darwin's \_Animals and Plants under Domestication\_,

vol. i. pp. 40-42.]

[Footnote 34: Mr. Brent in \_Journal of Horticulture\_, 1861, p. 76;

quoted by Darwin, \_Animals and Plants under Domestication\_, vol. i. p.

151.]

[Footnote 35: This account of domestic pigeons is greatly condensed from

Mr. Darwin's work already referred to.]

[Footnote 36: \_Animals and Plants under Domestication\_, vol. ii. pp.

307-311.]

CHAPTER V

NATURAL SELECTION BY VARIATION AND SURVIVAL OF THE FITTEST

Effect of struggle for existence under unchanged conditions--The

effect under change of conditions--Divergence of character--In

insects--In birds--In mammalia--Divergence leads to a maximum of

life in each area--Closely allied species inhabit distinct

areas--Adaptation to conditions at various periods of life--The

continued existence of low forms of life--Extinction of low

types among the higher animals--Circumstances favourable to the

origin of new species--Probable origin of the dippers--The

importance of isolation--On the advance of organisation by

natural selection--Summary of the first five chapters.

In the preceding chapters we have accumulated a body of facts and

arguments which will enable us now to deal with the very core of our

subject--the formation of species by means of natural selection. We have

seen how tremendous is the struggle for existence always going on in

nature owing to the great powers of increase of all organisms; we have

ascertained the fact of variability extending to every part and organ,

each of which varies simultaneously and for the most part independently;

and we have seen that this variability is both large in its amount in

proportion to the size of each part, and usually affects a considerable

proportion of the individuals in the large and dominant species. And,

lastly, we have seen how similar variations, occurring in cultivated

plants and domestic animals, are capable of being perpetuated and

accumulated by artificial selection, till they have resulted in all the

wonderful varieties of our fruits, flowers, and vegetables, our domestic

animals and household pets, many of which differ from each other far

more in external characters, habits, and instincts than do species in a

state of nature. We have now to inquire whether there is any analogous

process in nature, by which wild animals and plants can be permanently

modified and new races or new species produced.

\_Effect of Struggle for Existence under Unchanged Conditions.\_

Let us first consider what will be the effect of the struggle for

existence upon the animals and plants which we see around us, under

conditions which do not perceptibly vary from year to year or from

century to century. We have seen that every species is exposed to

numerous and varied dangers throughout its entire existence, and that it

is only by means of the exact adaptation of its organisation--including

its instincts and habits--to its surroundings that it is enabled to live

till it produces offspring which may take its place when it ceases to

exist. We have seen also that, of the whole annual increase only a very

small fraction survives; and though the survival in individual cases may

sometimes be due rather to accident than to any real superiority, yet we

cannot doubt that, in the long run, those survive which are best fitted

by their perfect organisation to escape the dangers that surround them.

This "survival of the fittest" is what Darwin termed "natural

selection," because it leads to the same results in nature as are

produced by man's selection among domestic animals and cultivated

plants. Its primary effect will, clearly, be to keep each species in the

most perfect health and vigour, with every part of its organisation in

full harmony with the conditions of its existence. It prevents any

possible deterioration in the organic world, and produces that

appearance of exuberant life and enjoyment, of health and beauty, that

affords us so much pleasure, and which might lead a superficial observer

to suppose that peace and quietude reigned throughout nature.

\_The Effect under changed Conditions.\_

But the very same process which, so long as conditions remain

substantially the same, secures the continuance of each species of

animal or plant in its full perfection, will usually, under changed

conditions, bring about whatever change of structure or habits may be

necessitated by them. The changed conditions to which we refer are such

as we know have occurred throughout all geological time and in every

part of the world. Land and water have been continually shifting their

positions; some regions are undergoing subsidence with diminution of

area, others elevation with extension of area; dry land has been

converted into marshes, while marshes have been drained or have even

been elevated into plateaux. Climate too has changed again and again,

either through the elevation of mountains in high latitudes leading to

the accumulation of snow and ice, or by a change in the direction of

winds and ocean currents produced by the subsidence or elevation of

lands which connected continents and divided oceans. Again, along with

all these changes have come not less important changes in the

distribution of species. Vegetation has been greatly modified by changes

of climate and of altitude; while every union of lands before separated

has led to extensive migrations of animals into new countries,

disturbing the balance that before existed among its forms of life,

leading to the extermination of some species and the increase of others.

When such physical changes as these have taken place, it is evident that

many species must either become modified or cease to exist. When the

vegetation has changed in character the herbivorous animals must become

able to live on new and perhaps less nutritious food; while the change

from a damp to a dry climate may necessitate migration at certain

periods to escape destruction by drought. This will expose the species

to new dangers, and require special modifications of structure to meet

them. Greater swiftness, increased cunning, nocturnal habits, change of

colour, or the power of climbing trees and living for a time on their

foliage or fruit, may be the means adopted by different species to bring

themselves into harmony with the new conditions; and by the continued

survival of those individuals, only, which varied sufficiently in the

right direction, the necessary modifications of structure or of function

would be brought about, just as surely as man has been able to breed the

greyhound to hunt by sight and the foxhound by scent, or has produced

from the same wild plant such distinct forms as the cauliflower and the

brussels sprouts.

We will now consider the special characteristics of the changes in

species that are likely to be effected, and how far they agree with what

we observe in nature.

\_Divergence of Character.\_

In species which have a wide range the struggle for existence will often

cause some individuals or groups of individuals to adopt new habits in

order to seize upon vacant places in nature where the struggle is less

severe. Some, living among extensive marshes, may adopt a more aquatic

mode of life; others, living where forests abound, may become more

arboreal. In either case we cannot doubt that the changes of structure

needed to adapt them to their new habits would soon be brought about,

because we know that variations in all the external organs and all their

separate parts are very abundant and are also considerable in amount.

That such divergence of character has actually occurred we have some

direct evidence. Mr. Darwin informs us that in the Catskill Mountains in

the United States there are two varieties of wolves, one with a light

greyhound-like form which pursues deer, the other more bulky with

shorter legs, which more frequently attacks sheep.[37] Another good

example is that of the insects in the island of Madeira, many of which

have either lost their wings or have had them so much reduced as to be

useless for flight, while the very same species on the continent of

Europe possess fully developed wings. In other cases the wingless

Madeira species are distinct from, but closely allied to, winged species

of Europe. The explanation of this change is, that Madeira, like many

oceanic islands in the temperate zone, is much exposed to sudden gales

of wind, and as most of the fertile land is on the coast, insects which

flew much would be very liable to be blown out to sea and lost. Year

after year, therefore, those individuals which had shorter wings, or

which used them least, were preserved; and thus, in time, terrestrial,

wingless, or imperfectly winged races or species have been produced.

That this is the true explanation of this singular fact is proved by

much corroborative evidence. There are some few flower-frequenting

insects in Madeira to whom wings are essential, and in these the wings

are somewhat larger than in the same species on the mainland. We thus

see that there is no general tendency to the abortion of wings in

Madeira, but that it is simply a case of adaptation to new conditions.

Those insects to whom wings were not absolutely essential escaped a

serious danger by not using them, and the wings therefore became reduced

or were completely lost. But when they were essential they were enlarged

and strengthened, so that the insect could battle against the winds and

save itself from destruction at sea. Many flying insects, not varying

fast enough, would be destroyed before they could establish themselves,

and thus we may explain the total absence from Madeira of several whole

families of winged insects which must have had many opportunities of

reaching the islands. Such are the large groups of the tiger-beetles

(Cicindelidae), the chafers (Melolonthidae), the click-beetles

(Elateridae), and many others.

But the most curious and striking confirmation of this portion of Mr.

Darwin's theory is afforded by the case of Kerguelen Island. This island

was visited by the \_Transit of Venus\_ expedition. It is one of the

stormiest places on the globe, being subject to almost perpetual gales,

while, there being no wood, it is almost entirely without shelter. The

Rev. A.E. Eaton, an experienced entomologist, was naturalist to the

expedition, and he assiduously collected the few insects that were to be

found. All were incapable of flight, and most of them entirely without

wings. They included a moth, several flies, and numerous beetles. As

these insects could hardly have reached the islands in a wingless state,

even if there were any other known land inhabited by them--which there

is not--we must assume that, like the Madeiran insects, they were

originally winged, and lost their power of flight because its possession

was injurious to them.

It is no doubt due to the same cause that some butterflies on small and

exposed islands have their wings reduced in size, as is strikingly the

case with the small tortoise-shell butterfly (Vanessa urticae)

inhabiting the Isle of Man, which is only about half the size of the

same species in England or Ireland; and Mr. Wollaston notes that Vanessa

callirhoe--a closely allied South European form of our red-admiral

butterfly--is permanently smaller in the small and bare island of Porto

Santo than in the larger and more wooded adjacent island of Madeira.

A very good example of comparatively recent divergence of character, in

accordance with new conditions of life, is afforded by our red grouse.

This bird, the Lagopus scoticus of naturalists, is entirely confined to

the British Isles. It is, however, very closely allied to the willow

grouse (Lagopus albus), a bird which ranges all over Europe, Northern

Asia, and North America, but which, unlike our species, changes to white

in winter. No difference in form or structure can be detected between

the two birds, but as they differ so decidedly in colour--our species

being usually rather darker in winter than in summer, while there are

also slight differences in the call-note and in habits,--the two species

are generally considered to be distinct. The differences, however, are

so clearly adaptations to changed conditions that we can hardly doubt

that, during the early part of the glacial period, when our islands were

united to the continent, our grouse was identical with that of the rest

of Europe. But when the cold passed away and our islands became

permanently separated from the mainland, with a mild and equable climate

and very little snow in winter, the change to white at that season

became hurtful, rendering the birds more conspicuous instead of serving

as a means of concealment. The colour was, therefore, gradually changed

by the process of variation and natural selection; and as the birds

obtained ample shelter among the heather which clothes so many of our

moorlands, it became useful for them to assimilate with its brown and

dusky stems and withered flowers rather than with the snow of the higher

mountains. An interesting confirmation of this change having really

occurred is afforded by the occasional occurrence in Scotland of birds

with a considerable amount of white in the winter plumage. This is

considered to be a case of reversion to the ancestral type, just as the

slaty colours and banded wings of the wild rock-pigeon sometimes

reappear in our fancy breeds of domestic pigeons.[38]

The principle of "divergence of character" pervades all nature from the

lowest groups to the highest, as may be well seen in the class of birds.

Among our native species we see it well marked in the different species

of titmice, pipits, and chats. The great titmouse (Parus major) by its

larger size and stronger bill is adapted to feed on larger insects, and

is even said sometimes to kill small and weak birds. The smaller and

weaker coal titmouse (Parus ater) has adopted a more vegetarian diet,

eating seeds as well as insects, and feeding on the ground as well as

among trees. The delicate little blue titmouse (Parus coeruleus), with

its very small bill, feeds on the minutest insects and grubs which it

extracts from crevices of bark and from the buds of fruit-trees. The

marsh titmouse, again (Parus palustris), has received its name from the

low and marshy localities it frequents; while the crested titmouse

(Parus cristatus) is a northern bird frequenting especially pine

forests, on the seeds of which trees it partially feeds. Then, again,

our three common pipits--the tree-pipit (Anthus arboreus), the

meadow-pipit (Anthus pratensis), and the rock-pipit or sea-lark (Anthus

obscurus) have each occupied a distinct place in nature to which they

have become specially adapted, as indicated by the different form and

size of the hind toe and claw in each species. So, the stone-chat

(Saxicola rubicola), the whin-chat (S. rubetra), and the wheat-ear (S.

oenanthe) are more or less divergent forms of one type, with

modifications in the shape of the wing, feet, and bill adapting them to

slightly different modes of life. The whin-chat is the smallest, and

frequents furzy commons, fields, and lowlands, feeding on worms,

insects, small molluscs, and berries; the stone-chat is next in size,

and is especially active and lively, frequenting heaths and uplands, and

is a permanent resident with us, the two other species being migrants;

while the larger and more conspicuous wheat-ear, besides feeding on

grubs, beetles, etc., is able to capture flying insects on the wing,

something after the manner of true flycatchers.

These examples sufficiently indicate how divergence of character has

acted, and has led to the adaptation of numerous allied species, each to

a more or less special mode of life, with the variety of food, of

habits, and of enemies which must necessarily accompany such diversity.

And when we extend our inquiries to higher groups we find the same

indications of divergence and special adaptation, often to a still more

marked extent. Thus we have the larger falcons, which prey upon birds,

while some of the smaller species, like the hobby (Falco subbuteo), live

largely on insects. The true falcons capture their prey in the air,

while the hawks usually seize it on or near the ground, feeding on

hares, rabbits, squirrels, grouse, pigeons, and poultry. Kites and

buzzards, on the other hand, seize their prey upon the ground, and the

former feed largely on reptiles and offal as well as on birds and

quadrupeds. Others have adopted fish as their chief food, and the osprey

snatches its prey from the water with as much facility as a gull or a

petrel; while the South American caracaras (Polyborus) have adopted the

habits of vultures and live altogether on carrion. In every great group

there is the same divergence of habits. There are ground-pigeons,

rock-pigeons, and wood-pigeons,--seed-eating pigeons and fruit-eating

pigeons; there are carrion-eating, insect-eating, and fruit-eating

crows. Even kingfishers are, some aquatic, some terrestrial in their

habits; some live on fish, some on insects, some on reptiles. Lastly,

among the primary divisions of birds we find a purely terrestrial

group--the Ratitae, including the ostriches, cassowaries, etc.; other

great groups, including the ducks, cormorants, gulls, penguins, etc.,

are aquatic; while the bulk of the Passerine birds are aerial and

arboreal. The same general facts can be detected in all other classes of

animals. In the mammalia, for example, we have in the common rat a

fish-eater and flesh-eater as well as a grain-eater, which has no doubt

helped to give it the power of spreading over the world and driving away

the native rats of other countries. Throughout the Rodent tribe we find

everywhere aquatic, terrestrial, and arboreal forms. In the weasel and

cat tribes some live more in trees, others on the ground; squirrels have

diverged into terrestrial, arboreal, and flying species; and finally, in

the bats we have a truly aerial, and in the whales a truly aquatic order

of mammals. We thus see that, beginning with different varieties of the

same species, we have allied species, genera, families, and orders, with

similarly divergent habits, and adaptations to different modes of life,

indicating some general principle in nature which has been operative in

the development of the organic world. But in order to be thus operative

it must be a generally useful principle, and Mr. Darwin has very clearly

shown us in what this utility consists.

\_Divergence leads to a Maximum of Organic Forms in each Area.\_

Divergence of character has a double purpose and use. In the first place

it enables a species which is being overcome by rivals, or is in

process of extinction by enemies, to save itself by adopting new habits

or by occupying vacant places in nature. This is the immediate and

obvious effect of all the numerous examples of divergence of character

which we have pointed out. But there is another and less obvious result,

which is, that the greater the diversity in the organisms inhabiting a

country or district the greater will be the total amount of life that

can be supported there. Hence the continued action of the struggle for

existence will tend to bring about more and more diversity in each area,

which may be shown to be the case by several kinds of evidence. As an

example, a piece of turf, three feet by four in size, was found by Mr.

Darwin to contain twenty species of plants, and these twenty species

belonged to eighteen genera and to eight orders, showing how greatly

they differed from each other. Farmers find that a greater quantity of

hay is obtained from ground sown with a variety of genera of grasses,

clover, etc., than from similar land sown with one or two species only;

and the same principle applies to rotation of crops, plants differing

very widely from each other giving the best results. So, in small and

uniform islands, and in small ponds of fresh water, the plants and

insects, though few in number, are found to be wonderfully varied in

character.

The same principle is seen in the naturalisation of plants and animals

by man's agency in distant lands, for the species that thrive best and

establish themselves permanently are not only very varied among

themselves but differ greatly from the native inhabitants. Thus, in the

Northern United States there are, according to Dr. Asa Gray, 260

naturalised flowering plants which belong to no less than 162 genera;

and of these, 100 genera are not natives of the United States. So, in

Australia, the rabbit, though totally unlike any native animal, has

increased so much that it probably outnumbers in individuals all the

native mammals of the country; and in New Zealand the rabbit and the pig

have equally multiplied. Darwin remarks that this "advantage of

diversification of structure in the inhabitants of the same region is,

in fact, the same as that of the physiological division of labour in the

organs of the same body. No physiologist doubts that a stomach adapted

to digest vegetable matter alone, or flesh alone, draws more nutriment

from these substances. So, in the general economy of any land, the more

widely and perfectly the animals and plants are diversified for

different habits of life, so will a greater number of individuals be

capable of there supporting themselves."[39]

\_The most closely allied Species inhabit distinct Areas.\_

One of the curious results of the general action of this principle in

nature is, that the most closely allied species--those whose differences

though often real and important are hardly perceptible to any one but a

naturalist--are usually not found in the same but in widely separated

countries. Thus, the nearest allies to our European golden plover are

found in North America and East Asia; the nearest ally of our European

jay is found in Japan, although there are several other species of jays

in Western Asia and North Africa; and though we have several species of

titmice in England they are not very closely allied to each other. The

form most akin to our blue tit is the azure tit of Central Asia (Parus

azureus); the Parus ledouci of Algeria is very near our coal tit, and

the Parus lugubris of South-Eastern Europe and Asia Minor is nearest to

our marsh tit. So, our four species of wild pigeons--the ring-dove,

stock-dove, rock-pigeon, and turtle-dove--are not closely allied to each

other, but each of them belongs, according to some ornithologists, to a

separate genus or subgenus, and has its nearest relatives in distant

parts of Asia and Africa. In mammalia the same thing occurs. Each

mountain region of Europe and Asia has usually its own species of wild

sheep and goat, and sometimes of antelope and deer; so that in each

region there is found the greatest diversity in this class of animals,

while the closest allies inhabit quite distinct and often distant areas.

In plants we find the same phenomenon prevalent. Distinct species of

columbine are found in Central Europe (Aguilegia vulgaris), in Eastern

Europe, and Siberia (A. glandulosa), in the Alps (A. Alpina), in the

Pyrenees (A. pyrenaiea), in the Greek mountains (A. ottonis), and in

Corsica (A. Bernardi), but rarely are two species found in the same

area. So, each part of the world has its own peculiar forms of pines,

firs, and cedars, but the closely allied species or varieties are in

almost every case inhabitants of distinct areas. Examples are the deodar

of the Himalayas, the cedar of Lebanon, and that of North Africa, all

very closely allied but confined to distinct areas; and the numerous

closely allied species of true pine (genus Pinus), which almost always

inhabit different countries or occupy different stations. We will now

consider some other modes in which natural selection will act, to adapt

organisms to changed conditions.

\_Adaptation to Conditions at Various Periods of Life.\_

It is found, that, in domestic animals and cultivated plants, variations

occurring at any one period of life reappear in the offspring at the

same period, and can be perpetuated and increased by selection without

modifying other parts of the organisation. Thus, variations in the

caterpillar or the cocoon of the silkworm, in the eggs of poultry, and

in the seeds or young shoots of many culinary vegetables, have been

accumulated till those parts have become greatly modified and, for man's

purposes, improved. Owing to this fact it is easy for organisms to

become so modified as to avoid dangers that occur at any one period of

life. Thus it is that so many seeds have become adapted to various modes

of dissemination or protection. Some are winged, or have down or hairs

attached to them, so as to enable them to be carried long distances in

the air; others have curious hooks and prickles, which cause them to be

attached firmly to the fur of mammals or the feathers of birds; while

others are buried within sweet or juicy and brightly coloured fruits,

which are seen and devoured by birds, the hard smooth seeds passing

through their bodies in a fit state for germination. In the struggle for

existence it must benefit a plant to have increased means of dispersing

its seeds, and of thus having young plants produced in a greater variety

of soils, aspects, and surroundings, with a greater chance of some of

them escaping their numerous enemies and arriving at maturity. The

various differences referred to would, therefore, be brought about by

variation and survival of the fittest, just as surely as the length and

quality of cotton on the seed of the cotton-plant have been increased

by man's selection.

The larvae of insects have thus been wonderfully modified in order to

escape the numerous enemies to whose attacks they are exposed at this

period of their existence. Their colours and markings have become

marvellously adapted to conceal them among the foliage of the plant they

live upon, and this colour often changes completely after the last

moult, when the creature has to descend to the ground for its change to

the pupa state, during which period a brown instead of a green colour is

protective. Others have acquired curious attitudes and large ocelli,

which cause them to resemble the head of some reptile, or they have

curious horns or coloured ejectile processes which frighten away

enemies; while a great number have acquired secretions which render them

offensive to the taste of their enemies, and these are always adorned

with very conspicuous markings or brilliant colours, which serve as a

sign of inedibility and prevent their being needlessly attacked. This,

however, is a portion of the very large subject of organic colour and

marking, which will be fully discussed and illustrated in a separate

chapter.

In this way every possible modification of an animal or plant, whether

in colour, form, structure, or habits, which would be serviceable to it

or to its progeny at any period of its existence, may be readily brought

about. There are some curious organs which are used only once in a

creature's life, but which are yet essential to its existence, and thus

have very much the appearance of design by an intelligent designer. Such

are, the great jaws possessed by some insects, used exclusively for

opening the cocoon, and the hard tip to the beak of unhatched birds used

for breaking the eggshell. The increase in thickness or hardness of the

cocoons or the eggs being useful for protection against enemies or to

avoid accidents, it is probable that the change has been very gradual,

because it would be constantly checked by the necessity for a

corresponding change in the young insects or birds enabling them to

overcome the additional obstacle of a tougher cocoon or a harder

eggshell. As we have seen, however, that every part of the organism

appears to be varying independently, at the same time, though to

different amounts, there seems no reason to believe that the necessity

for two or more coincident variations would prevent the required change

from taking place.

\_The Continued Existence of Low Forms of Life.\_

Since species are continually undergoing modifications giving them some

superiority over other species or enabling them to occupy fresh places

in nature, it may be asked--Why do any low forms continue to exist? Why

have they not long since been improved and developed into higher forms?

The answer, probably, is, that these low forms occupy places in nature

which cannot be filled by higher forms, and that they have few or no

competitors; they therefore continue to exist. Thus, earthworms are

adapted to their mode of life better than they would be if more highly

organised. So, in the ocean, the minute foraminifera and infusoria, and

the larger sponges and corals, occupy places which more highly developed

creatures could not fill. They form, as it were, the base of the great

structure of animal life, on which the next higher forms rest; and

though in the course of ages they may undergo some changes, and

diversification of form and structure, in accordance with changed

conditions, their essential nature has probably remained the same from

the very dawn of life on the earth. The low aquatic diatomaceae and

confervae, together with the lowest fungi and lichens, occupy a similar

position in the vegetable kingdom, filling places in nature which would

be left vacant if only highly organised plants existed. There is,

therefore, no motive power to destroy or seriously to modify them; and

they have thus probably persisted, under slightly varying forms, through

all geological time.

\_Extinction of Lower Types among the Higher Animals.\_

So soon; however, as we approach the higher and more fully developed

groups, we see indications of the often repeated extinction of lower by

higher forms. This is shown by the great gaps that separate the

mammalia, birds, reptiles, and fishes from each other; while the lowest

forms of each are always few in number and confined to limited areas.

Such are the lowest mammals--the echidna and ornithorhynchus of

Australia; the lowest birds--the apteryx of New Zealand and the

cassowaries of the New Guinea region; while the lowest fish--the

amphioxus or lancelet, is completely isolated, and has apparently

survived only by its habit of burrowing in the sand. The great

distinctness of the carnivora, ruminants, rodents, whales, bats, and

other orders of mammalia; of the accipitres, pigeons, and parrots, among

birds; and of the beetles, bees, flies, and moths, among insects, all

indicate an enormous amount of extinction among the comparatively low

forms by which, on any theory of evolution, these higher and more

specialised groups must have been preceded.

\_Circumstances favourable to the Origin of New Species by Natural

Selection.\_

We have already seen that, when there is no change in the physical or

organic conditions of a country, the effect of natural selection is to

keep all the species inhabiting it in a state of perfect health and full

development, and to preserve the balance that already exists between the

different groups of organisms. But, whenever the physical or organic

conditions change, to however small an extent, some corresponding change

will be produced in the flora and fauna, since, considering the severe

struggle for existence and the complex relations of the various

organisms, it is hardly possible that the change should not be

beneficial to some species and hurtful to others. The most common

effect, therefore, will be that some species will increase and others

will diminish; and in cases where a species was already small in numbers

a further diminution might lead to extinction. This would afford room

for the increase of other species, and thus a considerable readjustment

of the proportions of the several species might take place. When,

however, the change was of a more important character, directly

affecting the existence of many species so as to render it difficult for

them to maintain themselves without some considerable change in

structure or habits, that change would, in some cases, be brought about

by variation and natural selection, and thus new varieties or new

species might be formed. We have to consider, then, which are the

species that would be most likely to be so modified, while others, not

becoming modified, would succumb to the changed conditions and become

extinct.

The most important condition of all is, undoubtedly, that variations

should occur of sufficient amount, of a sufficiently diverse character,

and in a large number of individuals, so as to afford ample materials

for natural selection to act upon; and this, we have seen, does occur in

most, if not in all, large, wide-ranging, and dominant species. From

some of these, therefore, the new species adapted to the changed

conditions would usually be derived; and this would especially be the

case when the change of conditions was rather rapid, and when a

correspondingly rapid modification could alone save some species from

extinction. But when the change was very gradual, then even less

abundant and less widely distributed species might become modified into

new forms, more especially if the extinction of many of the rarer

species left vacant places in the economy of nature.

\_Probable Origin of the Dippers.\_

An excellent example of how a limited group of species has been able to

maintain itself by adaptation to one of these "vacant places" in nature,

is afforded by the curious little birds called dippers or water-ouzels,

forming the genus Cinclus and the family Cinclidae of naturalists. These

birds are something like small thrushes, with very short wings and tail,

and very dense plumage. They frequent, exclusively, mountain torrents in

the northern hemisphere, and obtain their food entirely in the water,

consisting, as it does, of water-beetles, caddis-worms and other

insect-larvae, as well as numerous small freshwater shells. These birds,

although not far removed in structure from thrushes and wrens, have the

extraordinary power of flying under water; for such, according to the

best observers, is their process of diving in search of their prey,

their dense and somewhat fibrous plumage retaining so much air that the

water is prevented from touching their bodies or even from wetting their

feathers to any great extent. Their powerful feet and long curved claws

enable them to hold on to stones at the bottom, and thus to retain their

position while picking up insects, shells, etc. As they frequent

chiefly the most rapid and boisterous torrents, among rocks, waterfalls,

and huge boulders, the water is never frozen over, and they are thus

able to live during the severest winters. Only a very few species of

dipper are known, all those of the old world being so closely allied to

our British bird that some ornithologists consider them to be merely

local races of one species; while in North America and the northern

Andes there are two other species.

Here then we have a bird, which, in its whole structure, shows a close

affinity to the smaller typical perching birds, but which has departed

from all its allies in its habits and mode of life, and has secured for

itself a place in nature where it has few competitors and few enemies.

We may well suppose, that, at some remote period, a bird which was

perhaps the common and more generalised ancestor of most of our

thrushes, warblers, wrens, etc., had spread widely over the great

northern continent, and had given rise to numerous varieties adapted to

special conditions of life. Among these some took to feeding on the

borders of clear streams, picking out such larvae and molluscs as they

could reach in shallow water. When food became scarce they would attempt

to pick them out of deeper and deeper water, and while doing this in

cold weather many would become frozen and starved. But any which

possessed denser and more hairy plumage than usual, which was able to

keep out the water, would survive; and thus a race would be formed which

would depend more and more on this kind of food. Then, following up the

frozen streams into the mountains, they would be able to live there

during the winter; and as such places afforded them much protection from

enemies and ample shelter for their nests and young, further adaptations

would occur, till the wonderful power of diving and flying under water

was acquired by a true land-bird.

That such habits might be acquired under stress of need is rendered

highly probable by the facts stated by the well-known American

naturalist, Dr. Abbott. He says that "the water-thrushes (Seiurus sp.)

all wade in water, and often, seeing minute mollusca on the bottom of

the stream, plunge both head and neck beneath the surface, so that

often, for several seconds, a large part of the body is submerged. Now

these birds still have the plumage pervious to water, and so are liable

to be drenched and sodden; but they have also the faculty of giving

these drenched feathers such a good shaking that flight is practicable a

moment after leaving the water. Certainly the water-thrushes (Seiurus

ludovicianus, S. auricapillus, and S. noveboracensis) have taken many

preliminary steps to becoming as aquatic as the dipper; and the

winter-wren, and even the Maryland yellow-throat are not far

behind."[40]

Another curious example of the way in which species have been modified

to occupy new places in nature, is afforded by the various animals which

inhabit the water-vessels formed by the leaves of many epiphytal species

of Bromelia. Fritz MÃ¼ller has described a caddis-fly larva which lives

among these leaves, and which has been modified in the pupa state in

accordance with its surroundings. The pupae of caddis-flies inhabiting

streams have fringes of hair on the tarsi to enable them to reach the

surface on leaving their cases. But in the species inhabiting bromelia

leaves there is no need for swimming, and accordingly we find the tarsi

entirely bare. In the same plants are found curious little Entomostraca,

very abundant there but found nowhere else. These form a new genus, but

are most nearly allied to Cythere, a marine type. It is believed that

the transmission of this species from one tree to another must be

effected by the young crustacea, which are very minute, clinging to

beetles, many of which, both terrestrial and aquatic, also inhabit the

bromelia leaves; and as some water-beetles are known to frequent the

sea, it is perhaps by these means that the first emigrants established

themselves in this strange new abode. Bromeliae are often very abundant

on trees growing on the water's edge, and this would facilitate the

transition from a marine to an arboreal habitat. Fritz MÃ¼ller has also

found, among the bromelia leaves, a small frog bearing its eggs on its

back, and having some other peculiarities of structure. Several

beautiful little aquatic plants of the genus Utricularia or bladder-wort

also inhabit bromelia leaves; and these send runners out to neighbouring

plants and thus spread themselves with great rapidity.

\_The Importance of Isolation.\_

Isolation is no doubt an important aid to natural selection, as shown by

the fact that islands so often present a number of peculiar species; and

the same thing is seen on the two sides of a great mountain range or on

opposite coasts of a continent. The importance of isolation is twofold.

In the first place, it leads to a body of individuals of each species

being limited in their range and thus subjected to uniform conditions

for long spaces of time. Both the direct action of the environment and

the natural selection of such varieties only as are suited to the

conditions, will, therefore, be able to produce their full effect. In

the second place, the process of change will not be interfered with by

intercrossing with other individuals which are becoming adapted to

somewhat different conditions in an adjacent area. But this question of

the swamping effects of intercrossing will be considered in another

chapter.

Mr. Darwin was of opinion that, on the whole, the largeness of the area

occupied by a species was of more importance than isolation, as a factor

in the production of new species, and in this I quite agree with him. It

must, too, be remembered, that isolation will often be produced in a

continuous area whenever a species becomes modified in accordance with

varied conditions or diverging habits. For example, a wide-ranging

species may in the northern and colder part of its area become modified

in one direction, and in the southern part in another direction; and

though for a long time an intermediate form may continue to exist in the

intervening area, this will be likely soon to die out, both because its

numbers will be small, and it will be more or less pressed upon in

varying seasons by the modified varieties, each better able to endure

extremes of climate. So, when one portion of a terrestrial species takes

to a more arboreal or to a more aquatic mode of life, the change of

habit itself leads to the isolation of each portion. Again, as will be

more fully explained in a future chapter, any difference of habits or of

haunts usually leads to some modification of colour or marking, as a

means of concealment from enemies; and there is reason to believe that

this difference will be intensified by natural selection as a means of

identification and recognition by members of the same variety or

incipient species. It has also been observed that each differently

coloured variety of wild animals, or of domesticated animals which have

run wild, keep together, and refuse to pair with individuals of the

other colours; and this must of itself act to keep the races separate as

completely as physical isolation.

\_On the Advance of Organisation by Natural Selection.\_

As natural selection acts solely by the preservation of useful

variations, or those which are beneficial to the organism under the

conditions to which it is exposed, the result must necessarily be that

each species or group tends to become more and more improved in relation

to its conditions. Hence we should expect that the larger groups in each

class of animals and plants--those which have persisted and have been

abundant throughout geological ages--would, almost necessarily, have

arrived at a high degree of organisation, both physical and mental.

Illustrations of this are to be seen everywhere. Among mammalia we have

the carnivora, which from Eocene times have been becoming more and more

specialised, till they have culminated in the cat and dog tribes, which

have reached a degree of perfection both in structure and intelligence

fully equal to that of any other animals. In another line of

development, the herbivora have been specialised for living solely on

vegetable food till they have culminated in the sheep, the cattle, the

deer, and the antelopes. The horse tribe, commencing with an early

four-toed ancestor in the Eocene age, has increased in size and in

perfect adaptation of feet and teeth to a life on open plains, and has

reached its highest perfection in the horse, the ass, and the zebra. In

birds, also, we see an advance from the imperfect tooth-billed and

reptile-tailed birds of the secondary epoch, to the wonderfully

developed falcons, crows, and swallows of our time. So, the ferns,

lycopods, conifers, and monocotyledons of the palaeozoic and mesozoic

rocks, have developed into the marvellous wealth of forms of the higher

dicotyledons that now adorn the earth.

But this remarkable advance in the higher and larger groups does not

imply any universal law of progress in organisation, because we have at

the same time numerous examples (as has been already pointed out) of the

persistence of lowly organised forms, and also of absolute degradation

or degeneration. Serpents, for example, have been developed from some

lizard-like type which has lost its limbs; and though this loss has

enabled them to occupy fresh places in nature and to increase and

flourish to a marvellous extent, yet it must be considered to be a

retrogression rather than an advance in organisation. The same remark

will apply to the whale tribe among mammals; to the blind amphibia and

insects of the great caverns; and among plants to the numerous cases in

which flowers, once specially adapted to be fertilised by insects, have

lost their gay corollas and their special adaptations, and have become

degraded into wind-fertilised forms. Such are our plantains, our meadow

burnet, and even, as some botanists maintain, our rushes, sedges, and

grasses. The causes which have led to this degeneration will be

discussed in a future chapter; but the facts are undisputed, and they

show us that although variation and the struggle for existence may lead,

on the whole, to a continued advance of organisation; yet they also lead

in many cases to a retrogression, when such retrogression may aid in the

preservation of any form under new conditions. They also lead to the

persistence, with slight modifications, of numerous lowly organised

forms which are suited to places which higher forms could not fully

occupy, or to conditions under which they could not exist. Such are the

ocean depths, the soil of the earth, the mud of rivers, deep caverns,

subterranean waters, etc.; and it is in such places as these, as well as

in some oceanic islands which competing higher forms have not been able

to reach, that we find many curious relics of an earlier world, which,

in the free air and sunlight and in the great continents, have long

since been driven out or exterminated by higher types.

\_Summary of the first Five Chapters.\_

We have now passed in review, in more or less detail, the main facts on

which the theory of "the origin of species by means of natural

selection" is founded. In future chapters we shall have to deal mainly

with the application of the theory to explain the varied and complex

phenomena presented by the organic world; and, also, to discuss some of

the theories put forth by modern writers, either as being more

fundamental than that of Darwin or as supplementary to it. Before doing

this, however, it will be well briefly to summarise the facts and

arguments already set forth, because it is only by a clear comprehension

of these that the full importance of the theory can be appreciated and

its further applications understood.

The theory itself is exceedingly simple, and the facts on which it

rests--though excessively numerous individually, and coextensive with

the entire organic world--yet come under a few simple and easily

understood classes. These facts are,--first, the enormous powers of

increase in geometrical progression possessed by all organisms, and the

inevitable struggle for existence among them; and, in the second place,

the occurrence of much individual variation combined with the hereditary

transmission of such variations. From these two great classes of facts,

which are universal and indisputable, there necessarily arises, as

Darwin termed it, the "preservation of favoured races in the struggle

for life," the continuous action of which, under the ever-changing

conditions both of the inorganic and organic universe, necessarily leads

to the formation or development of new species.

But, although this general statement is complete and indisputable, yet

to see its applications under all the complex conditions that actually

occur in nature, it is necessary always to bear in mind the tremendous

power and universality of the agencies at work. We must never for an

instant lose sight of the fact of the enormously rapid increase of all

organisms, which has been illustrated by actual cases, given in our

second chapter, no less than by calculations of the results of unchecked

increase for a few years. Then, never forgetting that the animal and

plant population of any country is, on the whole, stationary, we must be

always trying to realise the ever-recurring destruction of the enormous

annual increase, and asking ourselves what determines, in each

individual case, the death of the many, the survival of the few. We must

think over all the causes of destruction to each organism,--to the seed,

the young shoot, the growing plant, the full-grown tree, or shrub, or

herb, and again the fruit and seed; and among animals, to the egg or

new-born young, to the youthful, and to the adults. Then, we must always

bear in mind that what goes on in the case of the individual or family

group we may observe or think of, goes on also among the millions and

scores of millions of individuals which are comprised in almost every

species; and must get rid of the idea that \_chance\_ determines which

shall live and which die. For, although in many individual cases death

may be due to chance rather than to any inferiority in those which die

first, yet we cannot possibly believe that this can be the case on the

large scale on which nature works. A plant, for instance, cannot be

increased unless there are suitable vacant places its seeds can grow in,

or stations where it can overcome other less vigorous and healthy

plants. The seeds of all plants, by their varied modes of dispersal, may

be said to be seeking out such places in which to grow; and we cannot

doubt that, in the long run, those individuals whose seeds are the most

numerous, have the greatest powers of dispersal, and the greatest vigour

of growth, will leave more descendants than the individuals of the same

species which are inferior in all these respects, although now and then

some seed of an inferior individual may \_chance\_ to be carried to a spot

where it can grow and survive. The same rule will apply to every period

of life and to every danger to which plants or animals are exposed. The

best organised, or the most healthy, or the most active, or the best

protected, or the most intelligent, will inevitably, in the long run,

gain an advantage over those which are inferior in these qualities; that

is, \_the fittest will survive\_, the fittest being, in each particular

case, those which are superior in the special qualities on which safety

depends. At one period of life, or to escape one kind of danger,

concealment may be necessary; at another time, to escape another danger,

swiftness; at another, intelligence or cunning; at another, the power to

endure rain or cold or hunger; and those which possess all these

faculties in the fullest perfection will generally survive.

Having fully grasped these facts in all their fulness and in their

endless and complex results, we have next to consider the phenomena of

variation, discussed in the third and fourth chapters; and it is here

that perhaps the greatest difficulty will be felt in appreciating the

full importance of the evidence as set forth. It has been so generally

the practice to speak of variation as something exceptional and

comparatively rare--as an abnormal deviation from the uniformity and

stability of the characters of a species--and so few even among

naturalists have ever compared, accurately, considerable numbers of

individuals, that the conception of variability as a general

characteristic of all dominant and widespread species, large in its

amount and affecting, not a few, but considerable masses of the

individuals which make up the species, will be to many entirely new.

Equally important is the fact that the variability extends to every

organ and every structure, external and internal; while perhaps most

important of all is the independent variability of these several parts,

each one varying without any constant or even usual dependence on, or

correlation with, other parts. No doubt there is some such correlation

in the differences that exist between species and species--more

developed wings usually accompanying smaller feet and \_vice versÃ¢\_--but

this is, generally, a useful adaptation which has been brought about by

natural selection, and does not apply to the individual variability

which occurs within the species.

It is because these facts of variation are so important and so little

understood, that they have been discussed in what will seem to some

readers wearisome and unnecessary detail. Many naturalists, however,

will hold that even more evidence is required; and more, to almost any

amount, could easily have been given. The character and variety of that

already adduced will, however, I trust, convince most readers that the

facts are as stated; while they have been drawn from a sufficiently wide

area to indicate a general principle throughout nature.

If, now, we fully realise these facts of variation, along with those of

rapid multiplication and the struggle for existence, most of the

difficulties in the way of comprehending how species have originated

through natural selection will disappear. For whenever, through changes

of climate, or of altitude, or of the nature of the soil, or of the area

of the country, any species are exposed to new dangers, and have to

maintain themselves and provide for the safety of their offspring under

new and more arduous conditions, then, in the variability of all parts,

organs, and structures, no less than of habits and intelligence, we have

the means of producing modifications which will certainly bring the

species into harmony with its new conditions. And if we remember that

all such physical changes are slow and gradual in their operation, we

shall see that the amount of variation which we know occurs in every new

generation will be quite sufficient to enable modification and

adaptation to go on at the same rate. Mr. Darwin was rather inclined to

exaggerate the necessary slowness of the action of natural selection;

but with the knowledge we now possess of the great amount and range of

individual variation, there seems no difficulty in an amount of change,

quite equivalent to that which usually distinguishes allied species,

sometimes taking place in less than a century, should any rapid change

of conditions necessitate an equally rapid adaptation. This may often

have occurred, either to immigrants into a new land, or to residents

whose country has been cut off by subsidence from a larger and more

varied area over which they had formerly roamed. When no change of

conditions occurs, species may remain unchanged for very long periods,

and thus produce that appearance of stability of species which is even

now often adduced as an argument against evolution by natural selection,

but which is really quite in harmony with it.

On the principles, and by the light of the facts, now briefly

summarised, we have been able, in the present chapter, to indicate how

natural selection acts, how divergence of character is set up, how

adaptation to conditions at various periods of life has been effected,

how it is that low forms of life continue to exist, what kind of

circumstances are most favourable to the formation of new species, and,

lastly, to what extent the advance of organisation to higher types is

produced by natural selection. We will now pass on to consider some of

the more important objections and difficulties which have been advanced

by eminent naturalists.

FOOTNOTES:

[Footnote 37: \_Origin of Species\_, p. 71.]

[Footnote 38: Yarrell's \_British Birds\_, fourth edition, vol. iii. p.

77.]

[Footnote 39: \_Origin of Species\_, p. 89.]

[Footnote 40: \_Nature\_, vol. xxx. p. 30.]

CHAPTER VI

DIFFICULTIES AND OBJECTIONS

Difficulty as to smallness of variations--As to the right

variations occurring when required--The beginnings of important

organs--The mammary glands--The eyes of flatfish--Origin of the

eye--Useless or non-adaptive characters--Recent extension of the

region of utility in plants--The same in animals--Uses of

tails--Of the horns of deer--Of the scale-ornamentation of

reptiles--Instability of non-adaptive characters--Delboeuf's

law--No "specific" character proved to be useless--The swamping

effects of intercrossing--Isolation as preventing

intercrossing--Gulick on the effects of isolation--Cases in

which isolation is ineffective.

In the present chapter I propose to discuss the more obvious and often

repeated objections to Darwin's theory, and to show how far they affect

its character as a true and sufficient explanation of the origin of

species. The more recondite difficulties, affecting such fundamental

questions as the causes and laws of variability, will be left for a

future chapter, after we have become better acquainted with the

applications of the theory to the more important adaptations and

correlations of animal and plant life.

One of the earliest and most often repeated objections was, that it was

difficult "to imagine a reason why variations tending in an

infinitesimal degree in any special direction should be preserved," or

to believe that the complex adaptation of living organisms could have

been produced "by infinitesimal beginnings." Now this term

"infinitesimal," used by a well-known early critic of the \_Origin of

Species\_, was never made use of by Darwin himself, who spoke only of

variations being "slight," and of the "small amount" of the variations

that might be selected. Even in using these terms he undoubtedly

afforded grounds for the objection above made, that such small and

slight variations could be of no real use, and would not determine the

survival of the individuals possessing them. We have seen, however, in

our third chapter, that even Darwin's terms were hardly justified; and

that the variability of many important species is of considerable

amount, and may very often be properly described as large. As this is

found to be the case both in animals and plants, and in all their chief

groups and subdivisions, and also to apply to all the separate parts and

organs that have been compared, we must take it as proved that the

average \_amount\_ of variability presents no difficulty whatever in the

way of the action of natural selection. It may be here mentioned that,

up to the time of the preparation of the last edition of \_The Origin of

Species\_, Darwin had not seen the work of Mr. J.A. Allen of Harvard

University (then only just published), which gave us the first body of

accurate comparisons and measurements demonstrating this large amount of

variability. Since then evidence of this nature has been accumulating,

and we are, therefore, now in a far better position to appreciate the

facilities for natural selection, in this respect, than was Mr. Darwin

himself.

Another objection of a similar nature is, that the chances are immensely

against the right variation or combination of variations occurring just

when required; and further, that no variation can be perpetuated that is

not accompanied by several concomitant variations of dependent

parts--greater length of a wing in a bird, for example, would be of

little use if unaccompanied by increased volume or contractility of the

muscles which move it. This objection seemed a very strong one so long

as it was supposed that variations occurred singly and at considerable

intervals; but it ceases to have any weight now we know that they occur

simultaneously in various parts of the organism, and also in a large

proportion of the individuals which make up the species. A considerable

number of individuals will, therefore, every year possess the required

combination of characters; and it may also be considered probable that

when the two characters are such that they always \_act\_ together, there

will be such a correlation between them that they will frequently \_vary\_

together. But there is another consideration that seems to show that

this coincident variation is not essential. All animals in a state of

nature are kept, by the constant struggle for existence and the survival

of the fittest, in such a state of perfect health and usually

superabundant vigour, that in all ordinary circumstances they possess a

surplus power in every important organ--a surplus only drawn upon in

cases of the direst necessity when their very existence is at stake. It

follows, therefore, that \_any\_ additional power given to one of the

component parts of an organ must be useful--an increase, for example,

either in the wing muscles or in the form or length of the wing might

give \_some\_ increased powers of flight; and thus alternate

variations--in one generation in the muscles, in another generation in

the wing itself--might be as effective in permanently improving the

powers of flight as coincident variations at longer intervals. On either

supposition, however, this objection appears to have little weight if we

take into consideration the large amount of coincident variability that

has been shown to exist.

\_The Beginnings of Important Organs.\_

We now come to an objection which has perhaps been more frequently urged

than any other, and which Darwin himself felt to have much weight--the

first beginnings of important organs, such, for example, as wings, eyes,

mammary glands, and numerous other structures. It is urged, that it is

almost impossible to conceive how the first rudiments of these could

have been of any use, and, if not of use they could not have been

preserved and further developed by natural selection.

Now, the first remark to be made on objections of this nature is, that

they are really outside the question of the origin of all existing

species from allied species not very far removed from them, which is all

that Darwin undertook to \_prove\_ by means of his theory. Organs and

structures such as those above mentioned all date back to a very remote

past, when the world and its inhabitants were both very different from

what they are now. To ask of a new theory that it shall reveal to us

exactly what took place in remote geological epochs, and how it took

place, is unreasonable. The most that should be asked is, that some

probable or possible mode of origination should be pointed out in some

at least of these difficult cases, and this Mr. Darwin has done. One or

two of these may be briefly given here, but the whole series should be

carefully read by any one who wishes to see how many curious facts and

observations have been required in order to elucidate them; whence we

may conclude that further knowledge will probably throw light on any

difficulties that still remain.[41]

In the case of the mammary glands Mr. Darwin remarks that it is admitted

that the ancestral mammals were allied to the marsupials. Now in the

very earliest mammals, almost before they really deserved that name, the

young may have been nourished by a fluid secreted by the interior

surface of the marsupial sack, as is believed to be the case with the

fish (Hippocampus) whose eggs are hatched within a somewhat similar

sack. This being the case, those individuals which secreted a more

nutritious fluid, and those whose young were able to obtain and swallow

a more constant supply by suction, would be more likely to live and come

to a healthy maturity, and would therefore be preserved by natural

selection.

In another case which has been adduced as one of special difficulty, a

more complete explanation is given. Soles, turbots, and other flatfish

are, as is well known, unsymmetrical. They live and move on their sides,

the under side being usually differently coloured from that which is

kept uppermost. Now the eyes of these fish are curiously distorted in

order that both eyes may be on the upper side, where alone they would be

of any use. It was objected by Mr. Mivart that a sudden transformation

of the eye from one side to the other was inconceivable, while, if the

transit were gradual the first step could be of no use, since this would

not remove the eye from the lower side. But, as Mr. Darwin shows by

reference to the researches of Malm and others, the young of these fish

are quite symmetrical, and during their growth exhibit to us the whole

process of change. This begins by the fish (owing to the increasing

depth of the body) being unable to maintain the vertical position, so

that it falls on one side. It then twists the lower eye as much as

possible towards the upper side; and, the whole bony structure of the

head being at this time soft and flexible, the constant repetition of

this effort causes the eye gradually to move round the head till it

comes to the upper side. Now if we suppose this process, which in the

young is completed in a few days or weeks, to have been spread over

thousands of generations during the development of these fish, those

usually surviving whose eyes retained more and more of the position into

which the young fish tried to twist them, the change becomes

intelligible; though it still remains one of the most extraordinary

cases of degeneration, by which symmetry--which is so universal a

characteristic of the higher animals--is lost, in order that the

creature may be adapted to a new mode of life, whereby it is enabled the

better to escape danger and continue its existence.

The most difficult case of all, that of the eye--the thought of which

even to the last, Mr. Darwin says, "gave him a cold shiver"--is

nevertheless shown to be not unintelligible; granting of course the

sensitiveness to light of some forms of nervous tissue. For he shows

that there are, in several of the lower animals, rudiments of eyes,

consisting merely of pigment cells covered with a translucent skin,

which may possibly serve to distinguish light from darkness, but nothing

more. Then we have an optic nerve and pigment cells; then we find a

hollow filled with gelatinous substance of a convex form--the first

rudiment of a lens. Many of the succeeding steps are lost, as would

necessarily be the case, owing to the great advantage of each

modification which gave increased distinctness of vision, the creatures

possessing it inevitably surviving, while those below them became

extinct. But we can well understand how, after the first step was taken,

every variation tending to more complete vision would be preserved till

we reached the perfect eye of birds and mammals. Even this, as we know,

is not absolutely, but only relatively, perfect. Neither the chromatic

nor the spherical aberration is absolutely corrected; while long-and

short-sightedness, and the various diseases and imperfections to which

the eye is liable, may be looked upon as relics of the imperfect

condition from which the eye has been raised by variation and natural

selection.

These few examples of difficulties as to the origin of remarkable or

complex organs must suffice here; but the reader who wishes further

information on the matter may study carefully the whole of the sixth

and seventh chapters of the last edition of \_The Origin of Species\_, in

which these and many other cases are discussed in considerable detail.

\_Useless or non-adaptive Characters.\_

Many naturalists seem to be of opinion that a considerable number of the

characters which distinguish species are of no service whatever to their

possessors, and therefore cannot have been produced or increased by

natural selection. Professors Bronn and Broca have urged this objection

on the continent. In America, Dr. Cope, the well-known palaeontologist,

has long since put forth the same objection, declaring that non-adaptive

characters are as numerous as those which are adaptive; but he differs

completely from most who hold the same general opinion in considering

that they occur chiefly "in the characters of the classes, orders,

families, and other higher groups;" and the objection, therefore, is

quite distinct from that in which it is urged that "specific characters"

are mostly useless. More recently, Professor G.J. Romanes has urged this

difficulty in his paper on "Physiological Selection" (\_Journ. Linn.

Soc.\_, vol. xix. pp. 338, 344). He says that the characters "which serve

to distinguish allied species are frequently, if not usually, of a kind

with which natural selection can have had nothing to do," being without

any utilitarian significance. Again he speaks of "the enormous number,"

and further on of "the innumerable multitude" of specific peculiarities

which are useless; and he finally declares that the question needs no

further arguing, "because in the later editions of his works Mr. Darwin

freely acknowledges that a large proportion of specific distinctions

must be conceded to be useless to the species presenting them."

I have looked in vain in Mr. Darwin's works to find any such

acknowledgment, and I think Mr. Romanes has not sufficiently

distinguished between "useless characters" and "useless specific

distinctions." On referring to all the passages indicated by him I find

that, in regard to specific characters, Mr. Darwin is very cautious in

admitting inutility. His most pronounced "admissions" on this question

are the following: "But when, from the nature of the organism and of the

conditions, modifications have been induced which are unimportant for

the welfare of the species, they may be, and apparently often have been,

transmitted in nearly the same state \_to numerous, otherwise modified,

descendants\_" (\_Origin\_, p. 175). The words I have here italicised

clearly show that such characters are usually not "specific," in the

sense that they are such as distinguish species from each other, but are

found in numerous allied species. Again: "Thus a large yet undefined

extension may safely be given to the direct and indirect results of

natural selection; but I now admit, after reading the essay of NÃ¤geli on

plants, and the remarks by various authors with respect to animals, more

especially those recently made by Professor Broca, that in the earlier

editions of my \_Origin of Species\_ I perhaps attributed too much to the

action of natural selection or the survival of the fittest. I have

altered the fifth edition of the \_Origin\_ so as to confine my remarks to

adaptive changes of structure, \_but I am convinced, from the light

gained during even the last few years, that very many structures which

now appear to us useless, will hereafter be proved to be useful, and

will therefore come within the range of natural selection\_. Nevertheless

I did not formerly consider sufficiently the existence of structures

which, \_as far as we can at present judge\_, are neither beneficial nor

injurious; and this I believe to be one of the greatest oversights as

yet detected in my work." Now it is to be remarked that neither in these

passages nor in any of the other less distinct expressions of opinion on

this question, does Darwin ever admit that "specific characters"--that

is, the particular characters which serve to distinguish one species

from another--are ever useless, much less that "a large proportion of

them" are so, as Mr. Romanes makes him "freely acknowledge." On the

other hand, in the passage which I have italicised he strongly expresses

his view that much of what we suppose to be useless is due to our

ignorance; and as I hold myself that, as regards many of the supposed

useless characters, this is the true explanation, it may be well to give

a brief sketch of the progress of knowledge in transferring characters

from the one category to the other.

We have only to go back a single generation, and not even the most acute

botanist could have suggested a reasonable use, for each species of

plant, of the infinitely varied forms, sizes, and colours of the

flowers, the shapes and arrangement of the leaves, and the numerous

other external characters of the whole plant. But since Mr. Darwin

showed that plants gained both in vigour and in fertility by being

crossed with other individuals of the same species, and that this

crossing was usually effected by insects which, in search of nectar or

pollen, carried the pollen from one plant to the flowers of another

plant, almost every detail is found to have a purpose and a use. The

shape, the size, and the colour of the petals, even the streaks and

spots with which they are adorned, the position in which they stand, the

movements of the stamens and pistil at various times, especially at the

period of, and just after, fertilisation, have been proved to be

strictly adaptive in so many cases that botanists now believe that all

the external characters of flowers either are or have been of use to the

species.

It has also been shown, by Kerner and other botanists, that another set

of characteristics have relation to the prevention of ants, slugs, and

other animals from reaching the flowers, because these creatures would

devour or injure them without effecting fertilisation. The spines,

hairs, or sticky glands on the stem or flower-stalk, the curious hairs

or processes shutting up the flower, or sometimes even the extreme

smoothness and polish of the outside of the petals so that few insects

can hang to the part, have been shown to be related to the possible

intrusion of these "unbidden guests."[42] And, still more recently,

attempts have been made by Grant Allen and Sir John Lubbock to account

for the innumerable forms, textures, and groupings of leaves, by their

relation to the needs of the plants themselves; and there can be little

doubt that these attempts will be ultimately successful. Again, just as

flowers have been adapted to secure fertilisation or

cross-fertilisation, fruits have been developed to assist in the

dispersal of seeds; and their forms, sizes, juices, and colours can be

shown to be specially adapted to secure such dispersal by the agency of

birds and mammals; while the same end is secured in other cases by

downy seeds to be wafted through the air, or by hooked or sticky

seed-vessels to be carried away, attached to skin, wool, or feathers.

Here, then, we have an enormous extension of the region of utility in

the vegetable kingdom, and one, moreover, which includes almost all the

specific characters of plants. For the species of plants are usually

characterised either by differences in the form, size, and colour of the

flowers, or of the fruits; or, by peculiarities in the shape, size,

dentation, or arrangement of the leaves; or by peculiarities in the

spines, hairs, or down with which various parts of the plant are

clothed. In the case of plants it must certainly be admitted that

"specific" characters are pre-eminently adaptive; and though there may

be some which are not so, yet all those referred to by Darwin as having

been adduced by various botanists as useless, either pertain to genera

or higher groups, or are found in some plants of a species only--that

is, are individual variations not specific characters.

In the case of animals, the most recent wide extension of the sphere of

utility has been in the matter of their colours and markings. It was of

course always known that certain creatures gained protection by their

resemblance to their normal surroundings, as in the case of white arctic

animals, the yellow or brown tints of those living in deserts, and the

green hues of many birds and insects surrounded by tropical vegetation.

But of late years these cases have been greatly increased both in number

and variety, especially in regard to those which closely imitate special

objects among which they live; and there are other kinds of coloration

which long appeared to have no use. Large numbers of animals, more

especially insects, are gaudily coloured, either with vivid hues or with

striking patterns, so as to be very easily seen. Now it has been found,

that in almost all these cases the creatures possess some special

quality which prevents their being attacked by the enemies of their kind

whenever the peculiarity is known; and the brilliant or conspicuous

colours or markings serve as a warning or signal flag against attack.

Large numbers of insects thus coloured are nauseous and inedible;

others, like wasps and bees, have stings; others are too hard to be

eaten by small birds; while snakes with poisonous fangs often have some

characteristic either of rattle, hood, or unusual colour, which

indicates that they had better be left alone.

But there is yet another form of coloration, which consists in special

markings--bands, spots, or patches of white, or of bright colour, which

vary in every species, and are often concealed when the creature is at

rest but displayed when in motion,--as in the case of the bands and

spots so frequent on the wings and tails of birds. Now these specific

markings are believed, with good reason, to serve the purpose of

enabling each species to be quickly recognised, even at a distance, by

its fellows, especially the parents by their young and the two sexes by

each other; and this recognition must often be an important factor in

securing the safety of individuals, and therefore the wellbeing and

continuance of the species. These interesting peculiarities will be more

fully described in a future chapter, but they are briefly referred to

here in order to show that the most common of all the characters by

which species are distinguished from each other--their colours and

markings--can be shown to be adaptive or utilitarian in their nature.

But besides colour there are almost always some structural characters

which distinguish species from species, and, as regards many of these

also, an adaptive character can be often discerned. In birds, for

instance, we have differences in the size or shape of the bill or the

feet, in the length of the wing or the tail, and in the proportions of

the several feathers of which these organs are composed. All these

differences in the organs on which the very existence of birds depends,

which determine the character of flight, facility for running or

climbing, for inhabiting chiefly the ground or trees, and the kind of

food that can be most easily obtained for themselves and their

offspring, must surely be in the highest degree utilitarian; although in

each individual case we, in our ignorance of the minutiae of their

life-history, may be quite unable to see the use. In mammalia specific

differences other than colour usually consist in the length or shape of

the ears and tail, in the proportions of the limbs, or in the length and

quality of the hair on different parts of the body. As regards the ears

and tail, one of the objections by Professor Bronn relates to this very

point. He states that the length of these organs differ in the various

species of hares and of mice, and he considers that this difference can

be of no service whatever to their possessors. But to this objection

Darwin replies, that it has been shown by Dr. SchÃ¶bl that the ears of

mice "are supplied in an extraordinary manner with nerves, so that they

no doubt serve as tactile organs." Hence, when we consider the life of

mice, either nocturnal or seeking their food in dark and confined

places, the length of the ears may be in each case adapted to the

particular habits and surroundings of the species. Again, the tail, in

the larger mammals, often serves the purpose of driving off flies and

other insects from the body; and when we consider in how many parts of

the world flies are injurious or even fatal to large mammals, we see

that the peculiar characteristics of this organ may in each case have

been adapted to its requirements in the particular area where the

species was developed. The tail is also believed to have some use as a

balancing organ, which assists an animal to turn easily and rapidly,

much as our arms are used when running; while in whole groups it is a

prehensile organ, and has become modified in accordance with the habits

and needs of each species. In the case of mice it is thus used by the

young. Darwin informs us that the late Professor Henslow kept some

harvest-mice in confinement, and observed that they frequently curled

their tails round the branches of a bush placed in the cage, and thus

aided themselves in climbing; while Dr. GÃ¼nther has actually seen a

mouse suspend itself by the tail (\_Origin\_, p. 189).

Again, Mr. Lawson Tait has called attention to the use of the tail in

the cat, squirrel, yak, and many other animals as a means of preserving

the heat of the body during the nocturnal and the winter sleep. He says,

that in cold weather animals with long or bushy tails will be found

lying curled up, with their tails carefully laid over their feet like a

rug, and with their noses buried in the fur of the tail, which is thus

used exactly in the same way and for the same purpose as we use

respirators.[43]

Another illustration is furnished by the horns of deer which, especially

when very large, have been supposed to be a danger to the animal in

passing rapidly through dense thickets. But Sir James Hector states,

that the wapiti, in North America, throws back its head, thus placing

the horns along the sides of the back, and is then enabled to rush

through the thickest forest with great rapidity. The brow-antlers

protect the face and eyes, while the widely spreading horns prevent

injury to the neck or flanks. Thus an organ which was certainly

developed as a sexual weapon, has been so guided and modified during its

increase in size as to be of use in other ways. A similar use of the

antlers of deer has been observed in India.[44]

The various classes of facts now referred to serve to show us that, in

the case of the two higher groups--mammalia and birds--almost all the

characters by which species are distinguished from each other are, or

may be, adaptive. It is these two classes of animals which have been

most studied and whose life-histories are supposed to be most fully

known, yet even here the assertion of inutility, by an eminent

naturalist, in the case of two important organs, has been sufficiently

met by minute details either in the anatomy or in the habits of the

groups referred to. Such a fact as this, together with the extensive

series of characters already enumerated which have been of late years

transferred from the "useless" to the "useful" class, should convince

us, that the assertion of "inutility" in the case of any organ or

peculiarity which is not a rudiment or a correlation, is not, and can

never be, the statement of a fact, but merely an expression of our

ignorance of its purpose or origin.[45]

\_Instability of Non-adaptive Characters.\_

One very weighty objection to the theory that \_specific\_ characters can

ever be wholly useless (or wholly unconnected with useful organs by

correlation of growth) appears to have been overlooked by those who have

maintained the frequency of such characters, and that is, their almost

necessary instability. Darwin has remarked on the extreme variability of

secondary sexual characters--such as the horns, crests, plumes, etc.,

which are found in males only,--the reason being, that, although of some

use, they are not of such direct and vital importance as those adaptive

characters on which the wellbeing and very existence of the animals

depend. But in the case of wholly useless structures, which are not

rudiments of once useful organs, we cannot see what there is to ensure

any amount of constancy or stability. One of the cases on which Mr.

Romanes lays great stress in his paper on "Physiological Selection"

(\_Journ. Linn. Soc.\_, vol. xix. p. 384) is that of the fleshy appendages

on the corners of the jaw of Normandy pigs and of some other breeds. But

it is expressly stated that they are not constant; they appear

"frequently," or "occasionally," they are "not strictly inherited, for

they occur or fail in animals of the same litter;" and they are not

always symmetrical, sometimes appearing on one side of the face alone.

Now whatever may be the cause or explanation of these anomalous

appendages they cannot be classed with "specific characters," the most

essential features of which are, that they \_are\_ symmetrical, that they

\_are\_ inherited, and that they \_are\_ constant. Admitting that this

peculiar appendage is (as Mr. Romanes says rather confidently, "we

happen to know it to be") wholly useless and meaningless, the fact would

be rather an argument against specific characters being also

meaningless, because the latter never have the characteristics which

this particular variation possesses.

These useless or non-adaptive characters are, apparently, of the same

nature as the "sports" that arise in our domestic productions, but

which, as Mr. Darwin says, without the aid of selection would soon

disappear; while some of them may be correlations with other characters

which are or have been useful. Some of these correlations are very

curious. Mr. Tegetmeier informed Mr. Darwin that the young of white,

yellow, or dun-coloured pigeons are born almost naked, whereas other

coloured pigeons are born well clothed with down. Now, if this

difference occurred between wild species of different colours, it might

be said that the nakedness of the young could not be of any use. But the

colour with which it is correlated might, as has been shown, be useful

in many ways. The skin and its various appendages, as horns, hoofs,

hair, feathers, and teeth, are homologous parts, and are subject to very

strange correlations of growth. In Paraguay, horses with curled hair

occur, and these always have hoofs exactly like those of a mule, while

the hair of the mane and tail is much shorter than usual. Now, if any

one of these characters were useful, the others correlated with it might

be themselves useless, but would still be tolerably constant because

dependent on a useful organ. So the tusks and the bristles of the boar

are correlated and vary in development together, and the former only may

be useful, or both may be useful in unequal degrees.

The difficulty as to how individual differences or sports can become

fixed and perpetuated, if altogether useless, is evaded by those who

hold that such characters are exceedingly common. Mr. Romanes says that,

upon his theory of physiological selection, "it is quite intelligible

that when a varietal form is differentiated from its parent form by the

bar of sterility, any little meaningless peculiarities of structure or

of instinct \_should at first be allowed to arise\_, and that they should

then \_be allowed to perpetuate themselves\_ by heredity," until they are

finally eliminated by disuse. But this is entirely begging the

question. Do meaningless peculiarities, which we admit often arise as

spontaneous variations, ever perpetuate themselves in all the

individuals constituting a variety or race, without selection either

human or natural? Such characters present themselves as unstable

variations, and as such they remain, unless preserved and accumulated by

selection; and they can therefore never become "specific" characters

unless they are strictly correlated with some useful and important

peculiarities.

As bearing upon this question we may refer to what is termed Delboeuf's

law, which has been thus briefly stated by Mr. Murphy in his work on

\_Habit and Intelligence\_, p. 241.

"If, in any species, a number of individuals, bearing a ratio

not infinitely small to the entire number of births, are in

every generation born with a particular variation which is

neither beneficial nor injurious, and if it is not counteracted

by reversion, then the proportion of the new variety to the

original form will increase till it approaches indefinitely near

to equality."

It is not impossible that some definite varieties, such as the melanic

form of the jaguar and the bridled variety of the guillemot are due to

this cause; but from their very nature such varieties are unstable, and

are continually reproduced in varying proportions from the parent forms.

They can, therefore, never constitute species unless the variation in

question becomes beneficial, when it will be fixed by natural selection.

Darwin, it is true, says--"There can be little doubt that the tendency

to vary in the same manner has often been so strong that all the

individuals of the same species have been similarly modified without the

aid of any form of selection."[46] But no proof whatever is offered of

this statement, and it is so entirely opposed to all we know of the

facts of variation as given by Darwin himself, that the important word

"all" is probably an oversight.

On the whole, then, I submit, not only has it not been proved that an

"enormous number of specific peculiarities" are useless, and that, as a

logical result, natural selection is "not a theory of the origin of

species," but only of the origin of adaptations which are usually

common to many species, or, more commonly, to genera and families; but,

I urge further, it has not even been proved that any truly "specific"

characters--those which either singly or in combination distinguish each

species from its nearest allies--are entirely unadaptive, useless, and

meaningless; while a great body of facts on the one hand, and some

weighty arguments on the other, alike prove that specific characters

have been, and could only have been, developed and fixed by natural

selection because of their utility. We may admit, that among the great

number of variations and sports which continually arise many are

altogether useless without being hurtful; but no cause or influence has

been adduced adequate to render such characters fixed and constant

throughout the vast number of individuals which constitute any of the

more dominant species.[47]

\_The Swamping Effects of Intercrossing.\_

This supposed insuperable difficulty was first advanced in an article in

the \_North British Review\_ in 1867, and much attention has been

attracted to it by the acknowledgment of Mr. Darwin that it proved to

him that "single variations," or what are usually termed "sports," could

very rarely, if ever, be perpetuated in a state of nature, as he had at

first thought might occasionally be the case. But he had always

considered that the chief part, and latterly the whole, of the materials

with which natural selection works, was afforded by individual

variations, or that amount of ever fluctuating variability which exists

in all organisms and in all their parts. Other writers have urged the

same objection, even as against individual variability, apparently in

total ignorance of its amount and range; and quite recently Professor

G.J. Romanes has adduced it as one of the difficulties which can alone

be overcome by his theory of physiological selection. He urges, that the

same variation does not occur simultaneously in a number of individuals

inhabiting the same area, and that it is mere assumption to say it does;

while he admits that "if the assumption were granted there would be an

end of the present difficulty; for if a sufficient number of individuals

were thus simultaneously and similarly modified, there need be no longer

any danger of the variety becoming swamped by intercrossing." I must

again refer my readers to my third chapter for the proof that such

simultaneous variability is not an assumption but a fact; but, even

admitting this to be proved, the problem is not altogether solved, and

there is so much misconception regarding variation, and the actual

process of the origin of new species is so obscure, that some further

discussion and elucidation of the subject are desirable.

In one of the preliminary chapters of Mr. Seebohm's recent work on the

\_Charadriidae\_, he discusses the differentiation of species; and he

expresses a rather widespread view among naturalists when, speaking of

the swamping effects of intercrossing, he adds: "This is unquestionably

a very grave difficulty, to my mind an absolutely fatal one, to the

theory of accidental variation." And in another passage he says: "The

simultaneous appearance, and its repetition in successive generations,

of a beneficial variation, in a large number of individuals in the same

locality, cannot possibly be ascribed to chance." These remarks appear

to me to exhibit an entire misconception of the facts of variation as

they actually occur, and as they have been utilised by natural selection

in the modification of species. I have already shown that every part of

the organism, in common species, does vary to a very considerable

amount, in a large number of individuals, and in the same locality; the

only point that remains to be discussed is, whether any or most of these

variations are "beneficial." But every one of these variations consists

either in increase or diminution of size or power of the organ or

faculty that varies; they can all be divided into a more effective and a

less effective group--that is, into one that is more beneficial or less

beneficial. If less size of body would be beneficial, then, as half the

variations in size are above and half below the mean or existing

standard of the species, there would be ample beneficial variations; if

a darker colour or a longer beak or wing were required, there are always

a considerable number of individuals darker and lighter in colour than

the average, with longer or with shorter beaks and wings, and thus the

beneficial variation must always be present. And so with every other

part, organ, function, or habit; because, as variation, so far as we

know, is and always must be in the two directions of excess and defect

in relation to the mean amount, whichever kind of variation is wanted is

always present in some degree, and thus the difficulty as to

"beneficial" variations occurring, as if they were a special and rare

class, falls to the ground. No doubt some organs may vary in three or

perhaps more directions, as in the length, breadth, thickness, or

curvature of the bill. But these may be taken as separate variations,

each of which again occurs as "more" or "less"; and thus the "right" or

"beneficial" or "useful" variation must always be present so long as any

variation at all occurs; and it has not yet been proved that in any

large or dominant species, or in any part, organ, or faculty of such

species, there is no variation. And even were such a case found it would

prove nothing, so long as in numerous other species variation was shown

to exist; because we know that great numbers of species and groups

throughout all geological time have died out, leaving no descendants;

and the obvious and sufficient explanation of this fact is, that they

did \_not\_ vary enough at the time when variation was required to bring

them into harmony with changed conditions. The objection as to the

"right" or "beneficial" variation occurring when required, seems

therefore to have no weight in view of the actual facts of variation.

\_Isolation to prevent Intercrossing.\_

Most writers on the subject consider the isolation of a portion of a

species a very important factor in the formation of new species, while

others maintain it to be absolutely essential. This latter view has

arisen from an exaggerated opinion as to the power of intercrossing to

keep down any variety or incipient species, and merge it in the parent

stock. But it is evident that this can only occur with varieties which

are not useful, or which, if useful, occur in very small numbers; and

from this kind of variations it is clear that new species do not arise.

Complete isolation, as in an oceanic island, will no doubt enable

natural selection to act more rapidly, for several reasons. In the first

place, the absence of competition will for some time allow the new

immigrants to increase rapidly till they reach the limits of

subsistence. They will then struggle among themselves, and by survival

of the fittest will quickly become adapted to the new conditions of

their environment. Organs which they formerly needed, to defend

themselves against, or to escape from, enemies, being no longer

required, would be encumbrances to be got rid of, while the power of

appropriating and digesting new and varied food would rise in

importance. Thus we may explain the origin of so many flightless and

rather bulky birds in oceanic islands, as the dodo, the cassowary, and

the extinct moas. Again, while this process was going on, the complete

isolation would prevent its being checked by the immigration of new

competitors or enemies, which would be very likely to occur in a

continuous area; while, of course, any intercrossing with the original

unmodified stock would be absolutely prevented. If, now, before this

change has gone very far, the variety spreads into adjacent but rather

distant islands, the somewhat different conditions in each may lead to

the development of distinct forms constituting what are termed

representative species; and these we find in the separate islands of the

Galapagos, the West Indies, and other ancient groups of islands.

But such cases as these will only lead to the production of a few

peculiar species, descended from the original settlers which happened to

reach the islands; whereas, in wide areas, and in continents, we have

variation and adaptation on a much larger scale; and, whenever important

physical changes demand them, with even greater rapidity. The far

greater complexity of the environment, together with the occurrence of

variations in constitution and habits, will often allow of effective

isolation, even here, producing all the results of actual physical

isolation. As we have already explained, one of the most frequent modes

in which natural selection acts is, by adapting some individuals of a

species to a somewhat different mode of life, whereby they are able to

seize upon unappropriated places in nature, and in so doing they become

practically isolated from their parent form. Let us suppose, for

example, that one portion of a species usually living in forests ranges

into the open plains, and finding abundance of food remains there

permanently. So long as the struggle for existence is not exceptionally

severe, these two portions of the species may remain almost unchanged;

but suppose some fresh enemies are attracted to the plains by the

presence of these new immigrants, then variation and natural selection

would lead to the preservation of those individuals best able to cope

with the difficulty, and thus the open country form would become

modified into a marked variety or into a distinct species; and there

would evidently be little chance of this modification being checked by

intercrossing with the parent form which remained in the forest.

Another mode of isolation is brought about by the variety--either owing

to habits, climate, or constitutional change--breeding at a slightly

different time from the parent species. This is known to produce

complete isolation in the case of many varieties of plants. Yet another

mode of isolation is brought about by changes of colour, and by the fact

that in a wild state animals of similar colours prefer to keep together

and refuse to pair with individuals of another colour. The probable

reason and utility of this habit will be explained in another chapter,

but the fact is well illustrated by the cattle which have run wild in

the Falkland Islands. These are of several different colours, but each

colour keeps in a separate herd, often restricted to one part of the

island; and one of these varieties--the mouse-coloured--is said to breed

a month earlier than the others; so that if this variety inhabited a

larger area it might very soon be established as a distinct race or

species.[48] Of course where the change of habits or of station is still

greater, as when a terrestrial animal becomes sub-aquatic, or when

aquatic animals come to live in tree-tops, as with the frogs and

Crustacea described at p. 118, the danger of intercrossing is reduced to

a minimum.

Several writers, however, not content with the indirect effects of

isolation here indicated, maintain that it is in itself a cause of

modification, and ultimately of the origination of new species. This

was the keynote of Mr. Vernon Wollaston's essay on "Variation of

Species," published in 1856, and it is adopted by the Rev. J.G. Gulick

in his paper on "Diversity of Evolution under one Set of External

Conditions" (\_Journ. Linn. Soc. Zool.\_, vol. xi. p. 496). The idea seems

to be that there is an inherent tendency to variation in certain

divergent lines, and that when one portion of a species is isolated,

even though under identical conditions, that tendency sets up a

divergence which carries that portion farther and farther away from the

original species. This view is held to be supported by the case of the

land shells of the Sandwich Islands, which certainly present some very

remarkable phenomena. In this comparatively small area there are about

300 species of land shells, almost all of which belong to one family (or

sub-family), the Achatinellidae, found nowhere else in the world. The

interesting point is the extreme restriction of the species and

varieties. The average range of each species is only five or six miles,

while some are restricted to but one or two square miles, and only a

very few range over a whole island. The forest region that extends over

one of the mountain-ranges of the island of Oahu, is about forty miles

in length and five or six miles in breadth; and this small territory

furnishes about 175 species, represented by 700 or 800 varieties. Mr.

Gulick states, that the vegetation of the different valleys on the same

side of this range is much the same, yet each has a molluscan fauna

differing in some degree from that of any other. "We frequently find a

genus represented in several successive valleys by allied species,

sometimes feeding on the same, sometimes on different plants. In every

such case the valleys that are nearest to each other furnish the most

nearly allied forms; and a full set of the varieties of each species

presents a minute gradation of forms between the more divergent types

found in the more widely separated localities." He urges, that these

constant differences cannot be attributed to natural selection, because

they occur in different valleys on the same side of the mountain, where

food, climate, and enemies are the same; and also, because there is no

greater difference in passing from the rainy to the dry side of the

mountains than in passing from one valley to another on the same side

an equal distance apart. In a very lengthy paper, presented to the

Linnean Society last year, on "Divergent Evolution through Cumulative

Segregation," Mr. Gulick endeavours to work out his views into a

complete theory, the main point of which may perhaps be indicated by the

following passage: "No two portions of a species possess exactly the

same average character, and the initial differences are for ever

reacting on the environment and on each other in such a way as to ensure

increasing divergence in each successive generation as long as the

individuals of the two groups are kept from intercrossing."[49]

It need hardly be said that the views of Mr. Darwin and myself are

inconsistent with the notion that, if the environment were absolutely

similar for the two isolated portions of the species, any such necessary

and constant divergence would take place. It is an error to assume that

what seem to us identical conditions are really identical to such small

and delicate organisms as these land molluscs, of whose needs and

difficulties at each successive stage of their existence, from the

freshly-laid egg up to the adult animal, we are so profoundly ignorant.

The exact proportions of the various species of plants, the numbers of

each kind of insect or of bird, the peculiarities of more or less

exposure to sunshine or to wind at certain critical epochs, and other

slight differences which to us are absolutely immaterial and

unrecognisable, may be of the highest significance to these humble

creatures, and be quite sufficient to require some slight adjustments of

size, form, or colour, which natural selection will bring about. All we

know of the facts of variation leads us to believe that, without this

action of natural selection, there would be produced over the whole area

a series of inconstant varieties mingled together, not a distinct

segregation of forms each confined to its own limited area.

Mr. Darwin has shown that, in the distribution and modification of

species, the biological is of more importance than the physical

environment, the struggle with other organisms being often more severe

than that with the forces of nature. This is particularly evident in the

case of plants, many of which, when protected from competition, thrive

in a soil, climate, and atmosphere widely different from those of their

native habitat. Thus, many alpine plants only found near perpetual snow

thrive well in our gardens at the level of the sea; as do the tritomas

from the sultry plains of South Africa, the yuccas from the arid hills

of Texas and Mexico, and the fuchsias from the damp and dreary shores of

the Straits of Magellan. It has been well said that plants do not live

where they like, but where they can; and the same remark will apply to

the animal world. Horses and cattle run wild and thrive both in North

and South America; rabbits, once confined to the south of Europe, have

established themselves in our own country and in Australia; while the

domestic fowl, a native of tropical India, thrives well in every part of

the temperate zone.

If, then, we admit that when one portion of a species is separated from

the rest, there will necessarily be a slight difference in the average

characters of the two portions, it does not follow that this difference

has much if any effect upon the characteristics that are developed by a

long period of isolation. In the first place, the difference itself will

necessarily be very slight unless there is an exceptional amount of

variability in the species; and in the next place, if the average

characters of the species are the expression of its exact adaptation to

its whole environment, then, given a precisely similar environment, and

the isolated portion will inevitably be brought back to the same average

of characters. But, as a matter of fact, it is impossible that the

environment of the isolated portion can be exactly like that of the bulk

of the species. It cannot be so physically, since no two separated areas

can be absolutely alike in climate and soil; and even if these are the

same, the geographical features, size, contour, and relation to winds,

seas, and rivers, would certainly differ. Biologically, the differences

are sure to be considerable. The isolated portion of a species will

almost always be in a much smaller area than that occupied by the

species as a whole, hence it is at once in a different position as

regards its own kind. The proportions of all the other species of

animals and plants are also sure to differ in the two areas, and some

species will almost always be absent in the smaller which are present in

the larger country. These differences will act and react on the

isolated portion of the species. The struggle for existence will differ

in its severity and in its incidence from that which affects the bulk of

the species. The absence of some one insect or other creature inimical

to the young animal or plant may cause a vast difference in its

conditions of existence, and may necessitate a modification of its

external or internal characters in quite a different direction from that

which happened to be present in the average of the individuals which

were first isolated.

On the whole, then, we conclude that, while isolation is an important

factor in effecting some modification of species, it is so, not on

account of any effect produced, or influence exerted by isolation \_per

se\_, but because it is always and necessarily accompanied by a change of

environment, both physical and biological. Natural selection will then

begin to act in adapting the isolated portion to its new conditions, and

will do this the more quickly and the more effectually because of the

isolation. We have, however, seen reason to believe that geographical or

local isolation is by no means essential to the differentiation of

species, because the same result is brought about by the incipient

species acquiring different habits or frequenting a different station;

and also by the fact that different varieties of the same species are

known to prefer to pair with their like, and thus to bring about a

physiological isolation of the most effective kind. This part of the

subject will be again referred to when the very difficult problems

presented by hybridity are discussed.[50]

\_Cases in which Isolation is Ineffective.\_

One objection to the views of those who, like Mr. Gulick, believe

isolation itself to be a cause of modification of species deserves

attention, namely, the entire absence of change where, if this were a

\_vera causa\_, we should expect to find it. In Ireland we have an

excellent test case, for we know that it has been separated from Britain

since the end of the glacial epoch, certainly many thousand years. Yet

hardly one of its mammals, reptiles, or land molluscs has undergone the

slightest change, even although there is certainly a distinct difference

in the environment both inorganic and organic. That changes have not

occurred through natural selection, is perhaps due to the less severe

struggle for existence owing to the smaller number of competing species;

but, if isolation itself were an efficient cause, acting continuously

and cumulatively, it is incredible that a decided change should not have

been produced in thousands of years. That no such change has occurred in

this, and many other cases of isolation, seems to prove that it is not

in itself a cause of modification.

There yet remain a number of difficulties and objections relating to the

question of hybridity, which are so important as to require a separate

chapter for their adequate discussion.

FOOTNOTES:

[Footnote 41: See \_Origin of Species\_, pp. 176-198.]

[Footnote 42: See Kerner's \_Flowers and their Unbidden Guests\_ for

numerous other structures and peculiarities of plants which are shown to

be adaptive and useful.]

[Footnote 43: \_Nature\_, vol. xx. p. 603.]

[Footnote 44: \_Nature\_, vol. xxxviii. p. 328.]

[Footnote 45: A very remarkable illustration of function in an

apparently useless ornament is given by Semper. He says, "It is known

that the skin of reptiles encloses the body with scales. These scales

are distinguished by very various sculpturings, highly characteristic of

the different species. Irrespective of their systematic significance

they appear to be of no value in the life of the animal; indeed, they

are viewed as ornamental without regard to the fact that they are

microscopic and much too delicate to be visible to other animals of

their own species. It might, therefore, seem hopeless to show the

necessity for their existence on Darwinian principles, and to prove that

they are physiologically active organs. Nevertheless, recent

investigations on this point have furnished evidence that this is

possible.

"It is known that many reptiles, and above all the snakes, cast off the

whole skin at once, whereas human beings do so by degrees. If by any

accident they are prevented doing so, they infallibly die, because the

old skin has grown so tough and hard that it hinders the increase in

volume which is inseparable from the growth of the animal. The casting

of the skin is induced by the formation on the surface of the inner

epidermis, of a layer of very fine and equally distributed hairs, which

evidently serve the purpose of mechanically raising the old skin by

their rigidity and position. These hairs then may be designated as

\_casting hairs\_. That they are destined and calculated for this end is

evident to me from the fact established by Dr. Braun, that the casting

of the shells of the river crayfish is induced in exactly the same

manner by the formation of a coating of hairs which mechanically loosens

the old skin or shell from the new. Now the researches of Braun and

Cartier have shown that these casting hairs--which serve the same

purpose in two groups of animals so far apart in the systematic

scale--after the casting, are partly transformed into the concentric

stripes, sharp spikes, ridges, or warts which ornament the outer edges

of the skin-scales of reptiles or the carapace of crabs."[1] Professor

Semper adds that this example, with many others that might be quoted,

shows that we need not abandon the hope of explaining morphological

characters on Darwinian principles, although their nature is often

difficult to understand.

During a recent discussion of this question in the pages of \_Nature\_,

Mr. St. George Mivart adduces several examples of what he deems useless

specific characters. Among them are the aborted index finger of the

lemurine Potto, and the thumbless hands of Colobus and Ateles, the

"life-saving action" of either of which he thinks incredible. These

cases suggest two remarks. In the first place, they involve \_generic\_,

not \_specific\_, characters; and the three genera adduced are somewhat

isolated, implying considerable antiquity and the extinction of many

allied forms. This is important, because it affords ample time for great

changes of conditions since the structures in question originated; and

without a knowledge of these changes we can never safely assert that any

detail of structure could not have been useful. In the second place, all

three are cases of aborted or rudimentary organs; and these are admitted

to be explained by non-use, leading to diminution of size, a further

reduction being brought about by the action of the principle of economy

of growth. But, when so reduced, the rudiment might be inconvenient or

even hurtful, and then natural selection would aid in its complete

abortion; in other words, the abortion of the part would be \_useful\_,

and would therefore be subject to the law of survival of the fittest.

The genera Ateles and Colobus are two of the most purely arboreal types

of monkeys, and it is not difficult to conceive that the constant use of

the elongated fingers for climbing from tree to tree, and catching on to

branches while making great leaps, might require all the nervous energy

and muscular growth to be directed to the fingers, the small thumb

remaining useless. The case of the Potto is more difficult, both because

it is, presumably, a more ancient type, and its actual life-history and

habits are completely unknown. These cases are, therefore, not at all to

the point as proving that positive specific characters--not mere

rudiments characterising whole genera--are in any case useless.

Mr. Mivart further objects to the alleged rigidity of the action of

natural selection, because wounded or malformed animals have been found

which had evidently lived a considerable time in their imperfect

condition. But this simply proves that they were living under a

temporarily favourable environment, and that the real struggle for

existence, in their case, had not yet taken place. We must surely admit

that, when the pinch came, and when perfectly formed stoats were dying

for want of food, the one-footed animal, referred to by Mr. Mivart,

would be among the first to succumb; and the same remark will apply to

his abnormally toothed hares and rheumatic monkeys, which might,

nevertheless, get on very well under favourable conditions. The struggle

for existence, under which all animals and plants have been developed,

is intermittent, and exceedingly irregular in its incidence and

severity. It is most severe and fatal to the young; but when an animal

has once reached maturity, and especially when it has gained experience

by several years of an eventful existence, it may be able to maintain

itself under conditions which would be fatal to a young and

inexperienced creature of the same species. The examples adduced by Mr.

Mivart do not, therefore, in any way impugn the hardness of nature as a

taskmaster, or the extreme severity of the recurring struggle for

existence. (See \_Nature\_, vol. xxxix. p. 127.)]

[Footnote 46: \_Origin of Species,\_ p. 72.]

[Footnote 47: Darwin's latest expression of opinion on this question is

interesting, since it shows that he was inclined to return to his

earlier view of the general, or universal, utility of specific

characters. In a letter to Semper (30th Nov. 1878) he writes: "As our

knowledge advances, very slight differences, considered by systematists

as of no importance in structure, are continually found to be

functionally important; and I have been especially struck with this fact

in the case of plants, to which my observations have, of late years,

been confined. Therefore it seems to me rather rash to consider slight

differences between representative species, for instance, those

inhabiting the different islands of the same archipelago, as of no

functional importance, and as not in any way due to natural selection"

\_(Life of Darwin\_, vol. iii. p. 161).]

[Footnote 48: See \_Variation of Animals and Plants\_, vol. i. p. 86.]

[Footnote 49: \_Journal of the Linnean Society, Zoology,\_ vol. xx. p.

215.]

[Footnote 50: In Mr. Gulick's last paper (\_Journal of Linn. Soc. Zool.\_,

vol. xx. pp. 189-274) he discusses the various forms of isolation above

referred to, under no less than thirty-eight different divisions and

subdivisions, with an elaborate terminology, and he argues that these

will frequently bring about divergent evolution without any change in

the environment or any action of natural selection. The discussion of

the problem here given will, I believe, sufficiently expose the fallacy

of his contention; but his illustration of the varied and often

recondite modes by which practical isolation may be brought about, may

help to remove one of the popular difficulties in the way of the action

of natural selection in the origination of species.]

CHAPTER VII

ON THE INFERTILITY OF CROSSES BETWEEN DISTINCT SPECIES AND THE USUAL

STERILITY OF THEIR HYBRID OFFSPRING

Statement of the problem--Extreme susceptibility of the

reproductive functions--Reciprocal crosses--Individual

differences in respect to cross-fertilisation--Dimorphism and

trimorphism among plants--Cases of the fertility of hybrids and

of the infertility of mongrels--The effects of close

interbreeding--Mr. Huth's objections--Fertile hybrids among

animals--Fertility of hybrids among plants--Cases of sterility

of mongrels--Parallelism between crossing and change of

conditions--Remarks on the facts of hybridity--Sterility due to

changed conditions and usually correlated with other

characters--Correlation of colour with constitutional

peculiarities--The isolation of varieties by selective

association--The influence of natural selection upon sterility

and fertility--Physiological selection--Summary and concluding

remarks.

One of the greatest, or perhaps we may say the greatest, of all the

difficulties in the way of accepting the theory of natural selection as

a complete explanation of the origin of species, has been the remarkable

difference between varieties and species in respect of fertility when

crossed. Generally speaking, it may be said that the varieties of any

one species, however different they may be in external appearance, are

perfectly fertile when crossed, and their mongrel offspring are equally

fertile when bred among themselves; while distinct species, on the other

hand, however closely they may resemble each other externally, are

usually infertile when crossed, and their hybrid offspring absolutely

sterile. This used to be considered a fixed law of nature, constituting

the absolute test and criterion of a \_species\_ as distinct from a

\_variety\_; and so long as it was believed that species were separate

creations, or at all events had an origin quite distinct from that of

varieties, this law could have no exceptions, because, if any two

species had been found to be fertile when crossed and their hybrid

offspring to be also fertile, this fact would have been held to prove

them to be not \_species\_ but \_varieties\_. On the other hand, if two

varieties had been found to be infertile, or their mongrel offspring to

be sterile, then it would have been said: These are not varieties but

true species. Thus the old theory led to inevitable reasoning in a

circle; and what might be only a rather common fact was elevated into a

law which had no exceptions.

The elaborate and careful examination of the whole subject by Mr.

Darwin, who has brought together a vast mass of evidence from the

experience of agriculturists and horticulturists, as well as from

scientific experimenters, has demonstrated that there is no such fixed

law in nature as was formerly supposed. He shows us that crosses between

some varieties are infertile or even sterile, while crosses between some

species are quite fertile; and that there are besides a number of

curious phenomena connected with the subject which render it impossible

to believe that sterility is anything more than an incidental property

of species, due to the extreme delicacy and susceptibility of the

reproductive powers, and dependent on physiological causes we have not

yet been able to trace. Nevertheless, the fact remains that most species

which have hitherto been crossed produce sterile hybrids, as in the

well-known case of the mule; while almost all domestic varieties, when

crossed, produce offspring which are perfectly fertile among themselves.

I will now endeavour to give such a sketch of the subject as may enable

the reader to see something of the complexity of the problem, referring

him to Mr. Darwin's works for fuller details.

\_Extreme Susceptibility of the Reproductive Functions.\_

One of the most interesting facts, as showing how susceptible to changed

conditions or to slight constitutional changes are the reproductive

powers of animals, is the very general difficulty of getting those which

are kept in confinement to breed; and this is frequently the only bar to

domesticating wild species. Thus, elephants, bears, foxes, and numbers

of species of rodents, very rarely breed in confinement; while other

species do so more or less freely. Hawks, vultures, and owls hardly ever

breed in confinement; neither did the falcons kept for hawking ever

breed. Of the numerous small seed-eating birds kept in aviaries, hardly

any breed, neither do parrots. Gallinaceous birds usually breed freely

in confinement, but some do not; and even the guans and curassows, kept

tame by the South American Indians, never breed. This shows that change

of climate has nothing to do with the phenomenon; and, in fact, the same

species that refuse to breed in Europe do so, in almost every case, when

tamed or confined in their native countries. This inability to reproduce

is not due to ill-health, since many of these creatures are perfectly

vigorous and live very long.

With our true domestic animals, on the other hand, fertility is perfect,

and is very little affected by changed conditions. Thus, we see the

common fowl, a native of tropical India, living and multiplying in

almost every part of the world; and the same is the case with our

cattle, sheep, and goats, our dogs and horses, and especially with

domestic pigeons. It therefore seems probable, that this facility for

breeding under changed conditions was an original property of the

species which man has domesticated--a property which, more than any

other, enabled him to domesticate them. Yet, even with these, there is

evidence that great changes of conditions affect the fertility. In the

hot valleys of the Andes sheep are less fertile; while geese taken to

the high plateau of Bogota were at first almost sterile, but after some

generations recovered their fertility. These and many other facts seem

to show that, with the majority of animals, even a slight change of

conditions may produce infertility or sterility; and also that after a

time, when the animal has become thoroughly acclimatised, as it were, to

the new conditions, the infertility is in some cases diminished or

altogether ceases. It is stated by Bechstein that the canary was long

infertile, and it is only of late years that good breeding birds have

become common; but in this case no doubt selection has aided the change.

As showing that these phenomena depend on deep-seated causes and are of

a very general nature, it is interesting to note that they occur also

in the vegetable kingdom. Allowing for all the circumstances which are

known to prevent the production of seed, such as too great luxuriance of

foliage, too little or too much heat, or the absence of insects to

cross-fertilise the flowers, Mr. Darwin shows that many species which

grow and flower with us, apparently in perfect health, yet never produce

seed. Other plants are affected by very slight changes of conditions,

producing seed freely in one soil and not in another, though apparently

growing equally well in both; while, in some cases, a difference of

position even in the same garden produces a similar result.[51]

\_Reciprocal Crosses.\_

Another indication of the extreme delicacy of the adjustment between the

sexes, which is necessary to produce fertility, is afforded by the

behaviour of many species and varieties when reciprocally crossed. This

will be best illustrated by a few of the examples furnished us by Mr.

Darwin. The two distinct species of plants, Mirabilis jalapa and M.

longiflora, can be easily crossed, and will produce healthy and fertile

hybrids when the pollen of the latter is applied to the stigma of the

former plant. But the same experimenter, KÃ¶lreuter, tried in vain, more

than two hundred times during eight years, to cross them by applying the

pollen of M. jalapa to the stigma of M. longiflora. In other cases two

plants are so closely allied that some botanists class them as varieties

(as with Matthiola annua and M. glabra), and yet there is the same great

difference in the result when they are reciprocally crossed.

\_Individual Differences in respect to Cross-Fertilisation.\_

A still more remarkable illustration of the delicate balance of

organisation needful for reproduction, is afforded by the individual

differences of animals and plants, as regards both their power of

intercrossing with other individuals or other species, and the fertility

of the offspring thus produced. Among domestic animals, Darwin states

that it is by no means rare to find certain males and females which will

not breed together, though both are known to be perfectly fertile with

other males and females. Cases of this kind have occurred among horses,

cattle, pigs, dogs, and pigeons; and the experiment has been tried so

frequently that there can be no doubt of the fact. Professor G.J.

Romanes states that he has a number of additional cases of this

individual incompatibility, or of absolute sterility, between two

individuals, each of which is perfectly fertile with other individuals.

During the numerous experiments that have been made on the hybridisation

of plants similar peculiarities have been noticed, some individuals

being capable, others incapable, of being crossed with a distinct

species. The same individual peculiarities are found in varieties,

species, and genera. KÃ¶lreuter crossed five varieties of the common

tobacco (Nicotiana tabacum) with a distinct species, Nicotiana

glutinosa, and they all yielded very sterile hybrids; but those raised

from one variety were less sterile, in all the experiments, than the

hybrids from the four other varieties. Again, most of the species of the

genus Nicotiana have been crossed, and freely produce hybrids; but one

species, N. acuminata, not particularly distinct from the others, could

neither fertilise, nor be fertilised by, any of the eight other species

experimented on. Among genera we find some--such as Hippeastrum, Crinum,

Calceolaria, Dianthus--almost all the species of which will fertilise

other species and produce hybrid offspring; while other allied genera,

as Zephyranthes and Silene, notwithstanding the most persevering

efforts, have not produced a single hybrid even between the most closely

allied species.

\_Dimorphism and Trimorphism.\_

Peculiarities in the reproductive system affecting individuals of the

same species reach their maximum in what are called heterostyled, or

dimorphic and trimorphic flowers, the phenomena presented by which form

one of the most remarkable of Mr. Darwin's many discoveries. Our common

cowslip and primrose, as well as many other species of the genus

Primula, have two kinds of flowers in about equal proportions. In one

kind the stamens are short, being situated about the middle of the tube

of the corolla, while the style is long, the globular stigma appearing

just in the centre of the open flower. In the other kind the stamens are

long, appearing in the centre or throat of the flower, while the style

is short, the stigma being situated halfway down the tube at the same

level as the stamens in the other form. These two forms have long been

known to florists as the "pin-eyed" and the "thrum-eyed," but they are

called by Darwin the long-styled and short-styled forms (see woodcut).

[Illustration: FIG. 17.--Primula veris (Cowslip).]

The meaning and use of these different forms was quite unknown till

Darwin discovered, first, that cowslips and primroses are absolutely

barren if insects are prevented from visiting them, and then, what is

still more extraordinary, that each form is almost sterile when

fertilised by its own pollen, and comparatively infertile when crossed

with any other plant of its own form, but is perfectly fertile when the

pollen of a long-styled is carried to the stigma of a short-styled

plant, or \_vice versÃ¢\_. It will be seen, by the figures, that the

arrangement is such that a bee visiting the flowers will carry the

pollen from the long anthers of the short-styled form to the stigma of

the long-styled form, while it would never reach the stigma of another

plant of the short-styled form. But an insect visiting, first, a

long-styled plant, would deposit the pollen on the stigma of another

plant of the same kind if it were next visited; and this is probably the

reason why the wild short-styled plants were found to be almost always

most productive of seed, since they must be all fertilised by the other

form, whereas the long-styled plants might often be fertilised by their

own form. The whole arrangement, however, ensures cross-fertilisation;

and this, as Mr. Darwin has shown by copious experiments, adds both to

the vigour and fertility of almost all plants as well as animals.

Besides the primrose family, many other plants of several distinct

natural orders present similar phenomena, one or two of the most curious

of which must be referred to. The beautiful crimson flax (Linum

grandiflorum) has also two forms, the styles only differing in length;

and in this case Mr. Darwin found by numerous experiments, which have

since been repeated and confirmed by other observers, that each form is

absolutely sterile with pollen from another plant of its own form, but

abundantly fertile when crossed with any plant of the other form. In

this case the pollen of the two forms cannot be distinguished under the

microscope (whereas that of the two forms of Primula differs in size and

shape), yet it has the remarkable property of being absolutely powerless

on the stigmas of half the plants of its own species. The crosses

between the opposite forms, which are fertile, are termed by Mr. Darwin

"legitimate," and those between similar forms, which are sterile,

"illegitimate"; and he remarks that we have here, within the limits of

the same species, a degree of sterility which rarely occurs except

between plants or animals not only of different \_species\_ but of

different \_genera\_.

But there is another set of plants, the trimorphic, in which the styles

and stamens have each three forms--long, medium, and short, and in these

it is possible to have eighteen different crosses. By an elaborate

series of experiments it was shown that the six legitimate unions--that

is, when a plant was fertilised by pollen from stamens of length

corresponding to that of its style in the two other forms--were all

abundantly fertile; while the twelve illegitimate unions, when a plant

was fertilised by pollen from stamens of a different length from its

own style, in any of the three forms, were either comparatively or

wholly sterile.[52]

We have here a wonderful amount of constitutional difference of the

reproductive organs within a single species, greater than usually occurs

within the numerous distinct species of a genus or group of genera; and

all this diversity appears to have arisen for a purpose which has been

obtained by many other, and apparently simpler, changes of structure or

of function, in other plants. This seems to show us, in the first place,

that variations in the mutual relations of the reproductive organs of

different individuals must be as frequent as structural variations have

been shown to be; and, also, that sterility in itself can be no test of

specific distinctness. But this point will be better considered when we

have further illustrated and discussed the complex phenomena of

hybridity.

\_Cases of the Fertility of Hybrids, and of the Infertility of Mongrels.\_

I now propose to adduce a few cases in which it has been proved, by

experiment, that hybrids between two distinct species are fertile \_inter

se\_; and then to consider why it is that such cases are so few in

number.

The common domestic goose (Anser ferns) and the Chinese goose (A.

cygnoides) are very distinct species, so distinct that some naturalists

have placed them in different genera; yet they have bred together, and

Mr. Eyton raised from a pair of these hybrids a brood of eight. This

fact was confirmed by Mr. Darwin himself, who raised several fine birds

from a pair of hybrids which were sent him.[53] In India, according to

Mr. Blyth and Captain Hutton, whole flocks of these hybrid geese are

kept in various parts of the country where neither of the pure parent

species exists, and as they are kept for profit they must certainly be

fully fertile.

Another equally striking case is that of the Indian humped and the

common cattle, species which differ osteologically, and also in habits,

form, voice, and constitution, so that they are by no means closely

allied; yet Mr. Darwin assures us that he has received decisive

evidence that the hybrids between these are perfectly fertile \_inter

se\_.

Dogs have been frequently crossed with wolves and with jackals, and

their hybrid offspring have been found to be fertile \_inter se\_ to the

third or fourth generation, and then usually to show some signs of

sterility or of deterioration. The wolf and dog may be originally the

same species, but the jackal is certainly distinct; and the appearance

of infertility or of weakness is probably due to the fact that, in

almost all these experiments, the offspring of a single pair--themselves

usually from the same litter--- were bred in-and-in, and this alone

sometimes produces the most deleterious effects. Thus, Mr. Low in his

great work on the \_Domesticated Animals of Great Britain\_, says: "If we

shall breed a pair of dogs from the same litter, and unite again the

offspring of this pair, we shall produce at once a feeble race of

creatures; and the process being repeated for one or two generations

more, the family will die out, or be incapable of propagating their

race. A gentleman of Scotland made the experiment on a large scale with

certain foxhounds, and he found that the race actually became monstrous

and perished utterly." The same writer tells us that hogs have been made

the subject of similar experiments: "After a few generations the victims

manifest the change induced in the system. They become of diminished

size; the bristles are changed into hairs; the limbs become feeble and

short; the litters diminish in frequency, and in the number of the young

produced; the mother becomes unable to nourish them, and, if the

experiment be carried as far as the case will allow, the feeble, and

frequently monstrous offspring, will be incapable of being reared up,

and the miserable race will utterly perish."[54]

These precise statements, by one of the greatest authorities on our

domesticated animals, are sufficient to show that the fact of

infertility or degeneracy appearing in the offspring of hybrids after a

few generations need not be imputed to the fact of the first parents

being distinct species, since exactly the same phenomena appear when

individuals of the same species are bred under similar adverse

conditions. But in almost all the experiments that have hitherto been

made in crossing distinct species, no care has been taken to avoid close

interbreeding by securing several hybrids from quite distinct stocks to

start with, and by having two or more sets of experiments carried on at

once, so that crosses between the hybrids produced may be occasionally

made. Till this is done no experiments, such as those hitherto tried,

can be held to prove that hybrids are in all cases infertile \_inter se\_.

It has, however, been denied by Mr. A.H. Huth, in his interesting work

on \_The Marriage of Near Kin\_, that any amount of breeding in-and-in is

in itself hurtful; and he quotes the evidence of numerous breeders whose

choicest stocks have always been so bred, as well as cases like the

Porto Santo rabbits, the goats of Juan Fernandez, and other cases in

which animals allowed to run wild have increased prodigiously and

continued in perfect health and vigour, although all derived from a

single pair. But in all these cases there has been rigid selection by

which the weak or the infertile have been eliminated, and with such

selection there is no doubt that the ill effects of close interbreeding

can be prevented for a long time; but this by no means proves that no

ill effects are produced. Mr. Huth himself quotes M. AlliÃ©, M. AubÃ©,

Stephens, Giblett, Sir John Sebright, Youatt, Druce, Lord Weston, and

other eminent breeders, as finding from experience that close

interbreeding \_does\_ produce bad effects; and it cannot be supposed that

there would be such a consensus of opinion on this point if the evil

were altogether imaginary. Mr. Huth argues, that the evil results which

do occur do not depend on the close interbreeding itself, but on the

tendency it has to perpetuate any constitutional weakness or other

hereditary taints; and he attempts to prove this by the argument that

"if crosses act by virtue of being a cross, and not by virtue of

removing an hereditary taint, then the greater the difference between

the two animals crossed the more beneficial will that act be." He then

shows that, the wider the difference the less is the benefit, and

concludes that a cross, as such, has no beneficial effect. A parallel

argument would be, that change of air, as from inland to the sea-coast,

or from a low to an elevated site, is not beneficial in itself, because,

if so, a change to the tropics or to the polar regions should be more

beneficial. In both these cases it may well be that no benefit would

accrue to a person in perfect health; but then there is no such thing

as "perfect health" in man, and probably no such thing as absolute

freedom from constitutional taint in animals. The experiments of Mr.

Darwin, showing the great and immediate good effects of a cross between

distinct strains in plants, cannot be explained away; neither can the

innumerable arrangements to secure cross-fertilisation by insects, the

real use and purport of which will be discussed in our eleventh chapter.

On the whole, then, the evidence at our command proves that, whatever

may be its ultimate cause, close interbreeding \_does\_ usually produce

bad results; and it is only by the most rigid selection, whether natural

or artificial, that the danger can be altogether obviated.

\_Fertile Hybrids among Animals.\_

One or two more cases of fertile hybrids may be given before we pass on

to the corresponding experiments in plants. Professor Alfred Newton

received from a friend a pair of hybrid ducks, bred from a common duck

(Anas boschas), and a pintail (Dafila acuta). From these he obtained

four ducklings, but these latter, when grown up, proved infertile, and

did not breed again. In this case we have the results of close

interbreeding, with too great a difference between the original species,

combining to produce infertility, yet the fact of a hybrid from such a

pair producing healthy offspring is itself noteworthy.

Still more extraordinary is the following statement of Mr. Low: "It has

been long known to shepherds, though questioned by naturalists, that the

progeny of the cross between the sheep and goat is fertile. Breeds of

this mixed race are numerous in the north of Europe."[55] Nothing

appears to be known of such hybrids either in Scandinavia or in Italy;

but Professor Giglioli of Florence has kindly given me some useful

references to works in which they are described. The following extract

from his letter is very interesting: "I need not tell you that there

being such hybrids is now generally accepted as a fact. Buffon

(\_Supplements\_, tom. iii. p. 7, 1756) obtained one such hybrid in 1751

and eight in 1752. Sanson (\_La Culture\_, vol. vi. p. 372, 1865) mentions

a case observed in the Vosges, France. Geoff. St. Hilaire (\_Hist. Nat.

GÃ©n. des reg. org.\_, vol. iii. p. 163) was the first to mention, I

believe, that in different parts of South America the ram is more

usually crossed with the she-goat than the sheep with the he-goat. The

well-known 'pellones' of Chile are produced by the second and third

generation of such hybrids (Gay, 'Hist, de Chile,' vol. i. p. 466,

\_Agriculture\_, 1862). Hybrids bred from goat and sheep are called

'chabin' in French, and 'cabruno' in Spanish. In Chile such hybrids are

called 'carneros lanudos'; their breeding \_inter se\_ appears to be not

always successful, and often the original cross has to be recommenced to

obtain the proportion of three-eighths of he-goat and five-eighths of

sheep, or of three-eighths of ram and five-eighths of she-goat; such

being the reputed best hybrids."

With these numerous facts recorded by competent observers we can hardly

doubt that races of hybrids between these very distinct species have

been produced, and that such hybrids are fairly fertile \_inter se\_; and

the analogous facts already given lead us to believe that whatever

amount of infertility may at first exist could be eliminated by careful

selection, if the crossed races were bred in large numbers and over a

considerable area of country. This case is especially valuable, as

showing how careful we should be in assuming the infertility of hybrids

when experiments have been made with the progeny of a single pair, and

have been continued only for one or two generations.

Among insects one case only appears to have been recorded. The hybrids

of two moths (Bombyx cynthia and B. arrindia) were proved in Paris,

according to M. Quatrefages, to be fertile \_inter se\_ for eight

generations.

\_Fertility of Hybrids among Plants.\_

Among plants the cases of fertile hybrids are more numerous, owing, in

part, to the large scale on which they are grown by gardeners and

nurserymen, and to the greater facility with which experiments can be

made. Darwin tells us that KÃ¶lreuter found ten cases in which two plants

considered by botanists to be distinct species were quite fertile

together, and he therefore ranked them all as varieties of each other.

In some cases these were grown for six to ten successive generations,

but after a time the fertility decreased, as we saw to be the case in

animals, and presumably from the same cause, too close interbreeding.

Dean Herbert, who carried on experiments with great care and skill for

many years, found numerous cases of hybrids which were perfectly fertile

\_inter se\_. Crinum capense, fertilised by three other species--C.

pedunculatum, C. canaliculatum, or C. defixum--all very distinct from

it, produced perfectly fertile hybrids; while other species less

different in appearance were quite sterile with the same C. capense.

All the species of the genus Hippeastrum produce hybrid offspring which

are invariably fertile. Lobelia syphylitica and L. fulgens, two very

distinct species, have produced a hybrid which has been named Lobelia

speciosa, and which reproduces itself abundantly. Many of the beautiful

pelargoniums of our greenhouses are hybrids, such as P. ignescens from a

cross between P. citrinodorum and P. fulgidum, which is quite fertile,

and has become the parent of innumerable varieties of beautiful plants.

All the varied species of Calceolaria, however different in appearance,

intermix with the greatest readiness, and the hybrids are all more or

less fertile. But the most remarkable case is that of two species of

Petunia, of which Dean Herbert says: "It is very remarkable that,

although there is a great difference in the form of the flower,

especially of the tube, of P. nyctanigenaeflora and P. phoenicea the

mules between them are not only fertile, but I have found them seed much

more freely with me than either parent.... From a pod of the

above-mentioned mule, to which no pollen but its own had access, I had a

large batch of seedlings in which there was no variability or difference

from itself; and it is evident that the mule planted by itself, in a

congenial climate, would reproduce itself as a species; at least as much

deserving to be so considered as the various Calceolarias of different

districts of South America."[56]

Darwin was informed by Mr. C. Noble that he raises stocks for grafting

from a hybrid between Rhododendron ponticum and R. catawbiense, and that

this hybrid seeds as freely as it is possible to imagine. He adds that

horticulturists raise large beds of the same hybrid, and such alone are

fairly treated; for, by insect agency, the several individuals are

freely crossed with each other, and the injurious influence of close

interbreeding is thus prevented. Had hybrids, when fairly treated,

always gone on decreasing in fertility in each successive generation, as

Gartner believed to be the case, the fact would have been notorious to

nurserymen.[57]

\_Cases of Sterility of Mongrels.\_

The reverse phenomenon to the fertility of hybrids, the sterility of

mongrels or of the crosses between \_varieties\_ of the same species, is a

comparatively rare one, yet some undoubted cases have occurred. Gartner,

who believed in the absolute distinctness of species and varieties, had

two varieties of maize--one dwarf with yellow seeds, the other taller

with red seeds; yet they never naturally crossed, and, when fertilised

artificially, only a single head produced any seeds, and this one only

five grains. Yet these few seeds were fertile; so that in this case the

first cross was almost sterile, though the hybrid when at length

produced was fertile. In like manner, dissimilarly coloured varieties of

Verbascum or mullein have been found by two distinct observers to be

comparatively infertile. The two pimpernels (Anagallis arvensis and A.

coerulea), classed by most botanists as varieties of one species, have

been found, after repeated trials, to be perfectly sterile when crossed.

No cases of this kind are recorded among animals; but this is not to be

wondered at, when we consider how very few experiments have been made

with natural varieties; while there is good reason for believing that

domestic varieties are exceptionally fertile, partly because one of the

conditions of domestication was fertility under changed conditions, and

also because long continued domestication is believed to have the effect

of increasing fertility and eliminating whatever sterility may exist.

This is shown by the fact that, in many cases, domestic animals are

descended from two or more distinct species. This is almost certainly

the case with the dog, and probably with the hog, the ox, and the sheep;

yet the various breeds are now all perfectly fertile, although we have

every reason to suppose that there would be some degree of infertility

if the several aboriginal species were crossed together for the first

time.

\_Parallelism between Crossing and Change of Conditions.\_

In the whole series of these phenomena, from the beneficial effects of

the crossing of different stocks and the evil effects of close

interbreeding, up to the partial or complete sterility induced by

crosses between species belonging to different genera, we have, as Mr.

Darwin points out, a curious parallelism with the effects produced by

change of physical conditions. It is well known that slight changes in

the conditions of life are beneficial to all living things. Plants, if

constantly grown in one soil and locality from their own seeds, are

greatly benefited by the importation of seed from some other locality.

The same thing happens with animals; and the benefit we ourselves

experience from "change of air" is an illustration of the same

phenomenon. But the amount of the change which is beneficial has its

limits, and then a greater amount is injurious. A change to a climate a

few degrees warmer or colder may be good, while a change to the tropics

or to the arctic regions might be injurious.

Thus we see that, both slight changes of conditions and a slight amount

of crossing, are beneficial; while extreme changes, and crosses between

individuals too far removed in structure or constitution, are injurious.

And there is not only a parallelism but an actual connection between the

two classes of facts, for, as we have already shown, many species of

animals and plants are rendered infertile, or altogether sterile, by the

change from their natural conditions which occurs in confinement or in

cultivation; while, on the other hand, the increased vigour or fertility

which is invariably produced by a judicious cross may be also effected

by a judicious change of climate and surroundings. We shall see in a

subsequent chapter, that this interchangeability of the beneficial

effects of crossing and of new conditions, serves to explain some very

puzzling phenomena in the forms and economy of flowers.

\_Remarks on the Facts of Hybridity.\_

The facts that have now been adduced, though not very numerous, are

sufficiently conclusive to prove that the old belief, of the universal

sterility of hybrids and fertility of mongrels, is incorrect. The

doctrine that such a universal law existed was never more than a

plausible generalisation, founded on a few inconclusive facts derived

from domesticated animals and cultivated plants. The facts were, and

still are, inconclusive for several reasons. They are founded,

primarily, on what occurs among animals in domestication; and it has

been shown that domestication both tends to increase fertility, and was

itself rendered possible by the fertility of those particular species

being little affected by changed conditions. The exceptional fertility

of all the varieties of domesticated animals does not prove that a

similar fertility exists among natural varieties. In the next place, the

generalisation is founded on too remote crosses, as in the case of the

horse and the ass, the two most distinct and widely separated species of

the genus Equus, so distinct indeed that they have been held by some

naturalists to form distinct genera. Crosses between the two species of

zebra, or even between the zebra and the quagga, or the quagga and the

ass, might have led to a very different result. Again, in pre-Darwinian

times it was so universally the practice to argue in a circle, and

declare that the fertility of the offspring of a cross proved the

identity of species of the parents, that experiments in hybridity were

usually made between very remote species and even between species of

different genera, to avoid the possibility of the reply: "They are both

really the same species;" and the sterility of the hybrid offspring of

such remote crosses of course served to strengthen the popular belief.

Now that we have arrived at a different standpoint, and look upon a

species, not as a distinct entity due to special creation, but as an

assemblage of individuals which have become somewhat modified in

structure, form, and constitution so as to adapt them to slightly

different conditions of life; which can be differentiated from other

allied assemblages; which reproduce their like, and which usually breed

together--we require a fresh set of experiments calculated to determine

the matter of fact,--whether such species crossed with their near allies

do always produce offspring which are more or less sterile \_inter se\_.

Ample materials for such experiments exist, in the numerous

"representative species" inhabiting distinct areas on a continent or

different islands of a group; or even in those found in the same area

but frequenting somewhat different stations.

To carry out these experiments with any satisfactory result, it will be

necessary to avoid the evil effects of confinement and of too close

interbreeding. If birds are experimented with, they should be allowed as

much liberty as possible, a plot of ground with trees and bushes being

enclosed with wire netting overhead so as to form a large open aviary.

The species experimented with should be obtained in considerable

numbers, and by two separate persons, each making the opposite

reciprocal cross, as explained at p. 155. In the second generation these

two stocks might be themselves crossed to prevent the evil effects of

too close interbreeding. By such experiments, carefully carried out with

different groups of animals and plants, we should obtain a body of facts

of a character now sadly wanting, and without which it is hopeless to

expect to arrive at a complete solution of this difficult problem. There

are, however, some other aspects of the question that need to be

considered, and some theoretical views which require to be carefully

examined, having done which we shall be in a condition to state the

general conclusions to which the facts and reasonings at our command

seem to point.

\_Sterility due to changed Conditions and usually correlated with other

Characters, especially with Colour.\_

The evidence already adduced as to the extreme susceptibility of the

reproductive system, and the curious irregularity with which infertility

or sterility appears in the crosses between some varieties or species

while quite absent in those between others, seem to indicate that

sterility is a characteristic which has a constant tendency to appear,

either by itself or in correlation with other characters. It is known to

be especially liable to occur under changed conditions of life; and, as

such change is usually the starting-point and cause of the development

of new species, we have already found a reason why it should so often

appear when species become fully differentiated.

In almost all the cases of infertility or sterility between varieties or

species, we have some external differences with which it is correlated;

and though these differences are sometimes slight, and the amount of the

infertility is not always, or even usually, proportionate to the

external difference between the two forms crossed, we must believe that

there is some connection between the two classes of facts. This is

especially the case as regards colour; and Mr. Darwin has collected a

body of facts which go far to prove that colour, instead of being an

altogether trifling and unimportant character, as was supposed by the

older naturalists, is really one of great significance, since it is

undoubtedly often correlated with important constitutional differences.

Now colour is one of the characters that most usually distinguishes

closely allied species; and when we hear that the most closely allied

species of plants are infertile together, while those more remote are

fertile, the meaning usually is that the former differ chiefly in the

\_colour\_ of their flowers, while the latter differ in the form of the

flowers or foliage, in habit, or in other structural characters.

It is therefore a most curious and suggestive fact, that in all the

recorded cases, in which a decided infertility occurs between varieties

of the same species, those varieties are distinguished by a difference

of colour. The infertile varieties of Verbascum were white and yellow

flowered respectively; the infertile varieties of maize were red and

yellow seeded; while the infertile pimpernels were the red and the blue

flowered varieties. So, the differently coloured varieties of

hollyhocks, though grown close together, each reproduce their own colour

from seed, showing that they are not capable of freely intercrossing.

Yet Mr. Darwin assures us that the agency of bees is necessary to carry

the pollen from one plant to another, because in each flower the pollen

is shed before the stigma is ready to receive it. We have here,

therefore, either almost complete sterility between varieties of

different colours, or a prepotent effect of pollen from a flower of the

same colour, bringing about the same result.

Similar phenomena have not been recorded among animals; but this is not

to be wondered at when we consider that most of our pure and valued

domestic breeds are characterised by definite colours which constitute

one of their distinctive marks, and they are, therefore, seldom crossed

with these of another colour; and even when they are so crossed, no

notice would be taken of any slight diminution of fertility, since this

is liable to occur from many causes. We have also reason to believe that

fertility has been increased by long domestication, in addition to the

fact of the original stocks being exceptionally fertile; and no

experiments have been made on the differently coloured varieties of wild

animals. There are, however, a number of very curious facts showing that

colour in animals, as in plants, is often correlated with constitutional

differences of a remarkable kind, and as these have a close relation to

the subject we are discussing, a brief summary of them will be here

given.

\_Correlation of Colour with Constitutional Peculiarities.\_

The correlation of a white colour and blue eyes in male cats with

deafness, and of the tortoise-shell marking with the female sex of the

same animal, are two well-known but most extraordinary cases. Equally

remarkable is the fact, communicated to Darwin by Mr. Tegetmeier, that

white, yellow, pale blue, or dun pigeons, of all breeds, have the young

birds born naked, while in all other colours they are well covered with

down. Here we have a case in which colour seems of more physiological

importance than all the varied structural differences between the

varieties and breeds of pigeons. In Virginia there is a plant called the

paint-root (Lachnanthes tinctoria), which, when eaten by pigs, colours

their bones pink, and causes the hoofs of all but the black varieties to

drop off; so that black pigs only can be kept in the district.[58]

Buckwheat in flower is also said to be injurious to white pigs but not

to black. In the Tarentino, black sheep are not injured by eating the

Hypericum crispum--a species of St. John's-wort--which kills white

sheep. White terriers suffer most from distemper; white chickens from

the gapes. White-haired horses or cattle are subject to cutaneous

diseases from which the dark coloured are free; while, both in Thuringia

and the West Indies, it has been noticed that white or pale coloured

cattle are much more troubled by flies than are those which are brown or

black. The same law even extends to insects, for it is found that

silkworms which produce white cocoons resist the fungus disease much

better than do those which produce yellow cocoons.[59] Among plants, we

have in North America green and yellow-fruited plums not affected by a

disease that attacked the purple-fruited varieties. Yellow-fleshed

peaches suffer more from disease than white-fleshed kinds. In Mauritius,

white sugar-canes were attacked by a disease from which the red canes

were free. White onions and verbenas are most liable to mildew; and

red-flowered hyacinths were more injured by the cold during a severe

winter in Holland than any other kinds.[60]

These curious and inexplicable correlations of colour with

constitutional peculiarities, both in animals and plants, render it

probable that the correlation of colour with infertility, which has been

detected in several cases in plants, may also extend to animals in a

state of nature; and if so, the fact is of the highest importance as

throwing light on the origin of the infertility of many allied species.

This will be better understood after considering the facts which will be

now described.

\_The Isolation of Varieties by Selective Association.\_

In the last chapter I have shown that the importance of geographical

isolation for the formation of new species by natural selection has been

greatly exaggerated, because the very change of conditions, which is

the initial power in starting such new forms, leads also to a local or

stational segregation of the forms acted upon. But there is also a very

powerful cause of isolation in the mental nature--the likes and

dislikes--of animals; and to this is probably due the fact of the

comparative rarity of hybrids in a state of nature. The differently

coloured herds of cattle in the Falkland Islands, each of which keeps

separate, have been already mentioned; and it may be added, that the

mouse-coloured variety seem to have already developed a physiological

peculiarity in breeding a month earlier than the others. Similar facts

occur, however, among our domestic animals and are well known to

breeders. Professor Low, one of the greatest authorities on our

domesticated animals, says: "The female of the dog, when not under

restraint, makes selection of her mate, the mastiff selecting the

mastiff, the terrier the terrier, and so on." And again: "The Merino

sheep and Heath sheep of Scotland, if two flocks are mixed together,

each will breed with its own variety." Mr. Darwin has collected many

facts illustrating this point. One of the chief pigeon-fanciers in

England informed him that, if free to choose, each breed would prefer

pairing with its own kind. Among the wild horses in Paraguay those of

the same colour and size associate together; while in Circassia there

are three races of horses which have received special names, and which,

when living a free life, almost always refuse to mingle and cross, and

will even attack one another. On one of the Faroe Islands, not more than

half a mile in diameter, the half-wild native black sheep do not readily

mix with imported white sheep. In the Forest of Dean, and in the New

Forest, the dark and pale coloured herds of fallow deer have never been

known to mingle; and even the curious Ancon sheep of quite modern origin

have been observed to keep together, separating themselves from the rest

of the flock when put into enclosures with other sheep. The same rule

applies to birds, for Darwin was informed by the Rev. W.D. Fox that his

flocks of white and Chinese geese kept distinct.[61]

This constant preference of animals for their like, even in the case of

slightly different varieties of the same species, is evidently a fact

of great importance in considering the origin of species by natural

selection, since it shows us that, so soon as a slight differentiation

of form or colour has been effected, isolation will at once arise by the

selective association of the animals themselves; and thus the great

stumbling-block of "the swamping effects of intercrossing," which has

been so prominently brought forward by many naturalists, will be

completely obviated.

If now we combine with this fact the correlation of colour with

important constitutional peculiarities, and, in some cases, with

infertility; and consider, further, the curious parallelism that has

been shown to exist between the effects of changed conditions and the

intercrossing of varieties in producing either an increase or a decrease

of fertility, we shall have obtained, at all events, a starting-point

for the production of that infertility which is so characteristic a

feature of distinct species when intercrossed. All we need, now, is some

means of increasing or accumulating this initial tendency; and to a

discussion of this problem we will therefore address ourselves.

\_The Influence of Natural Selection upon Sterility and Fertility.\_

It will occur to many persons that, as the infertility or sterility of

incipient species would be useful to them when occupying the same or

adjacent areas, by neutralising the effects of intercrossing, this

infertility might have been increased by the action of natural

selection; and this will be thought the more probable if we admit, as we

have seen reason to do, that variations in fertility occur, perhaps as

frequently as other variations. Mr. Darwin tells us that, at one time,

this appeared to him probable, but he found the problem to be one of

extreme complexity; and he was also influenced against the view by many

considerations which seemed to render such an origin of the sterility or

infertility of species when intercrossed very improbable. The fact that

species which occupy distinct areas, and which nowhere come in contact

with each other, are often sterile when crossed, is one of the

difficulties; but this may perhaps be overcome by the consideration

that, though now isolated, they may, and often must, have been in

contact at their origination. More important is the objection that

natural selection could not possibly have produced the difference that

often occurs between reciprocal crosses, one of these being sometimes

fertile, while the other is sterile. The extremely different amounts of

infertility or sterility between different species of the same genus,

the infertility often bearing no proportion to the difference between

the species crossed, is also an important objection. But none of these

objections would have much weight if it could be clearly shown that

natural selection \_is\_ able to increase the infertility variations of

incipient species, as it is certainly able to increase and develop all

useful variations of form, structure, instincts, or habits. Ample causes

of infertility have been shown to exist, in the nature of the organism

and the laws of correlation; the agency of natural selection is only

needed to accumulate the effects produced by these causes, and to render

their final results more uniform and more in accordance with the facts

that exist.

About twenty years ago I had much correspondence and discussion with Mr.

Darwin on this question. I then believed that I was able to demonstrate

the action of natural selection in accumulating infertility; but I could

not convince him, owing to the extreme complexity of the process under

the conditions which he thought most probable. I have recently returned

to the question; and, with the fuller knowledge of the facts of

variation we now possess, I think it may be shown that natural selection

\_is\_, in some probable cases at all events, able to accumulate

variations in infertility between incipient species.

The simplest case to consider, will be that in which two forms or

varieties of a species, occupying an extensive area, are in process of

adaptation to somewhat different modes of life within the same area. If

these two forms freely intercross with each other, and produce mongrel

offspring which are quite fertile \_inter se\_, then the further

differentiation of the forms into two distinct species will be retarded,

or perhaps entirely prevented; for the offspring of the crossed unions

will be, perhaps, more vigorous on account of the cross, although less

perfectly adapted to the conditions of existence than either of the pure

breeds; and this would certainly establish a powerful antagonistic

influence to the further differentiation of the two forms.

Now, let us suppose that a partial sterility of the hybrids between the

two forms arises, in correlation with the different modes of life and

the slight external or internal peculiarities that exist between them,

both of which we have seen to be real causes of infertility. The result

will be that, even if the hybrids between the two forms are still freely

produced, these hybrids will not themselves increase so rapidly as the

two pure forms; and as these latter are, by the terms of the problem,

better suited to their conditions of life than are the hybrids between

them, they will not only increase more rapidly, but will also tend to

supplant the hybrids altogether whenever the struggle for existence

becomes exceptionally severe. Thus, the more complete the sterility of

the hybrids the more rapidly will they die out and leave the two parent

forms pure. Hence it will follow that, if there is greater infertility

between the two forms in one part of the area than the other, these

forms will be kept more pure wherever this greater infertility prevails,

will therefore have an advantage at each recurring period of severe

struggle for existence, and will thus ultimately supplant the less

infertile or completely fertile forms that may exist in other portions

of the area. It thus appears that, in such a case as here supposed,

natural selection would preserve those portions of the two breeds which

were most infertile with each other, or whose hybrid offspring were most

infertile; and would, therefore, if variations in fertility continued to

arise, tend to increase that infertility. It must particularly be noted

that this effect would result, not by the preservation of the infertile

variations on account of their infertility, but by the inferiority of

the hybrid offspring, both as being fewer in numbers, less able to

continue their race, and less adapted to the conditions of existence

than either of the pure forms. It is this inferiority of the hybrid

offspring that is the essential point; and as the number of these

hybrids will be permanently less where the infertility is greatest,

therefore those portions of the two forms in which infertility is

greatest will have the advantage, and will ultimately survive in the

struggle for existence.

The differentiation of the two forms into distinct species, with the

increase of infertility between them, would be greatly assisted by two

other important factors in the problem. It has already been shown that,

with each modification of form and habits, and especially with

modifications of colour, there arises a disinclination of the two forms

to pair together; and this would produce an amount of isolation which

would greatly assist the specialisation of the forms in adaptation to

their different conditions of life. Again, evidence has been adduced

that change of conditions or of mode of life is a potent cause of

disturbance of the reproductive system, and, consequently, of

infertility. We may therefore assume that, as the two forms adopted more

and more different modes of life, and perhaps acquired also decided

peculiarities of form and coloration, the infertility between them would

increase or become more general; and as we have seen that every such

increase of infertility would give that portion of the species in which

it arose an advantage over the remaining portions in which the two

varieties were more fertile together, all this induced infertility would

maintain itself, and still further increase the general infertility

between the two forms of the species.

It follows, then, that specialisation to separate conditions of life,

differentiation of external characters, disinclination to cross-unions,

and the infertility of the hybrid produce of these unions, would all

proceed \_pari passu\_, and would ultimately lead to the production of two

distinct forms having all the characteristics, physiological as well as

structural, of true species.

In the case now discussed it has been supposed, that some amount of

general infertility might arise in correlation with the different modes

of life of two varieties or incipient species. A considerable body of

facts already adduced renders it probable that this \_is\_ the mode in

which any widespread infertility would arise; and, if so, it has been

shown that, by the influence of natural selection and the known laws

which affect varieties, the infertility would be gradually increased.

But, if we suppose the infertility to arise sporadically within the two

forms, and to affect only a small proportion of the individuals in any

area, it will be difficult, if not impossible, to show that such

infertility would have any tendency to increase, or would produce any

but a prejudicial effect. If, for example, five per cent of each form

thus varied so as to be infertile with the other form, the result would

be hardly perceptible, because the individuals which formed cross-unions

and produced hybrids would constitute a very small portion of the whole

species; and the hybrid offspring, being at a disadvantage in the

struggle for existence and being themselves infertile, would soon die

out, while the much more numerous fertile portion of the two forms would

increase rapidly, and furnish a sufficient number of pure-bred offspring

of each form to take the place of the somewhat inferior hybrids between

them whenever the struggle for existence became severe. We must suppose

that the normal fertile forms would transmit their fertility to their

progeny, and the few infertile forms their infertility; but the latter

would necessarily lose half their proper increase by the sterility of

their hybrid offspring whenever they crossed with the other form, and

when they bred with their own form the tendency to sterility would die

out except in the very minute proportion of the five per cent

(one-twentieth) that chance would lead to pair together. Under these

circumstances the incipient sterility between the two forms would

rapidly be eliminated, and could never rise much above the numbers which

were produced by sporadic variation each year.

It was, probably, by a consideration of some such case as this that Mr.

Darwin came to the conclusion that infertility arising between incipient

species could not be increased by natural selection; and this is the

more likely, as he was always disposed to minimise both the frequency

and the amount even of structural variations.

We have yet to notice another mode of action of natural selection in

favouring and perpetuating any infertility that may arise between two

incipient species. If several distinct species are undergoing

modification at the same time and in the same area, to adapt them to

some new conditions that have arisen there, then any species in which

the structural or colour differences that have arisen between it and its

varieties or close allies were correlated with infertility of the

crosses between them, would have an advantage over the corresponding

varieties of other species in which there was no such physiological

peculiarity. Thus, incipient species which were infertile together would

have an advantage over other incipient species which were fertile, and,

whenever the struggle for existence became severe, would prevail over

them and take their place. Such infertility, being correlated with

constitutional or structural differences, would probably, as already

suggested, go on increasing as these differences increased; and thus, by

the time the new species became fully differentiated from its parent

form (or brother variety) the infertility might have become as well

marked as we usually find it to be between distinct species.

This discussion has led us to some conclusions of the greatest

importance as bearing on the difficult problem of the cause of the

sterility of the hybrids between distinct species. Accepting, as highly

probable, the fact of variations in fertility occurring in correlation

with variations in habits, colour, or structure, we see, that so long as

such variations occurred only sporadically, and affected but a small

proportion of the individuals in any area, the infertility could not be

increased by natural selection, but would tend to die out almost as fast

as it was produced. If, however, it was so closely correlated with

physical variations or diverse modes of life as to affect, even in a

small degree, a considerable proportion of the individuals of the two

forms in definite areas, it would be preserved by natural selection, and

the portion of the varying species thus affected would increase at the

expense of those portions which were more fertile when crossed. Each

further variation towards infertility between the two forms would be

again preserved, and thus the incipient infertility of the hybrid

offspring might be increased till it became so great as almost to amount

to sterility. Yet further, we have seen that if several competing

species in the same area were being simultaneously modified, those

between whose varieties infertility arose would have an advantage over

those whose varieties remained fertile \_inter se\_, and would ultimately

supplant them.

The preceding argument, it will be seen, depends entirely upon the

assumption that some amount of infertility characterises the distinct

varieties which are in process of differentiation into species; and it

may be objected that of such infertility there is no proof. This is

admitted; but it is urged that facts have been adduced which render such

infertility probable, at least in some cases, and this is all that is

required. It is by no means necessary that \_all\_ varieties should

exhibit incipient infertility, but only, some varieties; for we know

that, of the innumerable varieties that occur but few become developed

into distinct species, and it may be that the absence of infertility, to

obviate the effects of intercrossing, is one of the usual causes of

their failure. All I have attempted to show is, that \_when\_ incipient

infertility does occur in correlation with other varietal differences,

that infertility can be, and in fact must be, increased by natural

selection; and this, it appears to me, is a decided step in advance in

the solution of the problem.[62]

\_Physiological Selection.\_

Another form of infertility has been suggested by Professor G.J. Romanes

as having aided in bringing about the characteristic infertility or

sterility of hybrids. It is founded on the fact, already noticed, that

certain individuals of some species possess what may be termed selective

sterility--that is, while fertile with some individuals of the species

they are sterile with others, and this altogether independently of any

differences of form, colour, or structure. The phenomenon, in the only

form in which it has been observed, is that of "infertility or absolute

sterility between two individuals, each of which is perfectly fertile

with all other individuals;" but Mr. Romanes thinks that "it would not

be nearly so remarkable, or physiologically improbable, that such

incompatibility should run through a whole race or strain."[63]

Admitting that this may be so, though we have at present no evidence

whatever in support of it, it remains to be considered whether such

physiological varieties could maintain themselves, or whether, as in the

cases of sporadic infertility already discussed, they would necessarily

die out unless correlated with useful characters. Mr. Romanes thinks

that they would persist, and urges that "whenever this one kind of

variation occurs \_it cannot escape the preserving agency\_ of

physiological selection. Hence, even if it be granted that the variation

which affects the reproductive system in this particular way is a

variation of comparatively rare occurrence, still, as \_it must always be

preserved\_ whenever it does occur, its influence in the manufacture of

specific types \_must be cumulative\_." The very positive statements which

I have italicised would lead most readers to believe that the alleged

fact had been demonstrated by a careful working out of the process in

some definite supposed cases. This, however, has nowhere been done in

Mr. Romanes' paper; and as it is \_the\_ vital theoretical point on which

any possible value of the new theory rests, and as it appears so opposed

to the self-destructive effects of simple infertility, which we have

already demonstrated when it occurs between the intermingled portion of

two varieties, it must be carefully examined. In doing so, I will

suppose that the required variation is not of "rare occurrence," but of

considerable amount, and that it appears afresh each year to about the

same extent, thus giving the theory every possible advantage.

Let us then suppose that a given species consists of 100,000 individuals

of each sex, with only the usual amount of fluctuating external

variability. Let a physiological variation arise, so that 10 per cent of

the whole number--10,000 individuals of each sex--while remaining

fertile \_inter se\_ become quite sterile with the remaining 90,000. This

peculiarity is not correlated with any external differences of form or

colour, or with inherent peculiarities of likes or dislikes leading to

any choice as to the pairing of the two sets of individuals. We have now

to inquire, What would be the result?

Taking, first, the 10,000 pairs of the physiological or abnormal

variety, we find that each male of these might pair with any one of the

whole 100,000 of the opposite sex. If, therefore, there was nothing to

limit their choice to particular individuals of either variety, the

probabilities are that 9000 of them would pair with the opposite

variety, and only 1000 with their own variety--that is, that 9000 would

form sterile unions, and only \_one\_ thousand would form fertile unions.

Taking, next, the 90,000 normal individuals of either sex, we find, that

each male of these has also a choice of 100,000 to pair with. The

probabilities are, therefore, that nine-tenths of them--that is,

81,000--would pair with their normal fellows, while 9000 would pair with

the opposite abnormal variety forming the above-mentioned sterile

unions.

Now, as the number of individuals forming a species remains constant,

generally speaking, from year to year, we shall have next year also

100,000 pairs, of which the two physiological varieties will be in the

proportion of eighty-one to one, or 98,780 pairs of the normal variety

to 1220[64] of the abnormal, that being the proportion of the fertile

unions of each. In this year we shall find, by the same rule of

probabilities, that only 15 males of the abnormal variety will pair with

their like and be fertile, the remaining 1205 forming sterile unions

with some of the normal variety. The following year the total 100,000

pairs will consist of 99,984 of the normal, and only 16 of the abnormal

variety; and the probabilities, of course, are, that the whole of these

latter will pair with some of the enormous preponderance of normal

individuals, and, their unions being sterile, the physiological variety

will become extinct in the third year.

If now in the second and each succeeding year a similar proportion as at

first (10 per cent) of the physiological variety is produced afresh from

the ranks of the normal variety, the same rate of diminution will go on,

and it will be found that, on the most favourable estimate, the

physiological variety can never exceed 12,000 to the 88,000 of the

normal form of the species, as shown by the following table:--

1st Year. 10,000 of physiological variety to 90,000 of normal variety.

2d " 1,220 + 10,000 again produced.

3d " 16 + 1,220 + 10,000 do. = 11,236

4th " O + 16 + 1,220 + 10,000 do. = 11,236

5th " O + 16 + 1,220 + 10,000 = 11,236

and so on for any number of generations.

In the preceding discussion we have given the theory the advantage of

the large proportion of 10 per cent of this very exceptional variety

arising in its midst year by year, and we have seen that, even under

these favourable conditions, it is unable to increase its numbers much

above its starting-point, and that it remains wholly dependent on the

continued renewal of the variety for its existence beyond a few years.

It appears, then, that this form of inter-specific sterility cannot be

increased by natural or any other known form of selection, but that it

contains within itself its own principle of destruction. If it is

proposed to get over the difficulty by postulating a larger percentage

of the variety annually arising within the species, we shall not affect

the law of decrease until we approach equality in the numbers of the two

varieties. But with any such increase of the physiological variety the

species itself would inevitably suffer by the large proportion of

sterile unions in its midst, and would thus be at a great disadvantage

in competition with other species which were fertile throughout. Thus,

natural selection will always tend to weed out any species with too

great a tendency to sterility among its own members, and will therefore

prevent such sterility from becoming the general characteristic of

varying species, which this theory demands should be the case.

On the whole, then, it appears clear that no form of infertility or

sterility between the individuals of a species, can be increased by

natural selection unless correlated with some useful variation, while

all infertility not so correlated has a constant tendency to effect its

own elimination. But the opposite property, fertility, is of vital

importance to every species, and gives the offspring of the individuals

which possess it, in consequence of their superior numbers, a greater

chance of survival in the battle of life. It is, therefore, directly

under the control of natural selection, which acts both by the

self-preservation of fertile and the self-destruction of infertile

stocks--except always where correlated as above, when they become

useful, and therefore subject to be increased by natural selection.

\_Summary and Concluding Remarks on Hybridity.\_

The facts which are of the greatest importance to a comprehension of

this very difficult subject are those which show the extreme

susceptibility of the reproductive system both in plants and animals. We

have seen how both these classes of organisms may be rendered infertile,

by a change of conditions which does not affect their general health, by

captivity, or by too close interbreeding. We have seen, also, that

infertility is frequently correlated with a difference of colour, or

with other characters; that it is not proportionate to divergence of

structure; that it varies in reciprocal crosses between pairs of the

same species; while in the cases of dimorphic and trimorphic plants the

different crosses between the same pair of individuals may be fertile or

sterile at the same time. It appears as if fertility depended on such a

delicate adjustment of the male and female elements to each other, that,

unless constantly kept up by the preservation of the most fertile

individuals, sterility is always liable to arise. This preservation

always occurs within the limits of each species, both because fertility

is of the highest importance to the continuance of the race, and also

because sterility (and to a less extent infertility) is self-destructive

as well as injurious to the species.

So long therefore as a species remains undivided, and in occupation of a

continuous area, its fertility is kept up by natural selection; but the

moment it becomes separated, either by geographical or selective

isolation, or by diversity of station or of habits, then, while each

portion must be kept fertile \_inter se\_, there is nothing to prevent

infertility arising between the two separated portions. As the two

portions will necessarily exist under somewhat different conditions of

life, and will usually have acquired some diversity of form and

colour--both which circumstances we know to be either the cause of

infertility or to be correlated with it,--the fact of some degree of

infertility usually appearing between closely allied but locally or

physiologically segregated species is exactly what we should expect.

The reason why varieties do not usually exhibit a similar amount of

infertility is not difficult to explain. The popular conclusions on this

matter have been drawn chiefly from what occurs among domestic animals,

and we have seen that the very first essential to their becoming

domesticated was that they should continue fertile under changed

conditions of life. During the slow process of the formation of new

varieties by conscious or unconscious selection, fertility has always

been an essential character, and has thus been invariably preserved or

increased; while there is some evidence to show that domestication

itself tends to increase fertility.

Among plants, wild species and varieties have been more frequently

experimented on than among animals, and we accordingly find numerous

cases in which distinct species of plants are perfectly fertile when

crossed, their hybrid offspring being also fertile \_inter se\_. We also

find some few examples of the converse fact--varieties of the same

species which when crossed are infertile or even sterile.

The idea that either infertility or geographical isolation is absolutely

essential to the formation of new species, in order to prevent the

swamping effects of intercrossing, has been shown to be unsound, because

the varieties or incipient species will, in most cases, be sufficiently

isolated by having adopted different habits or by frequenting different

stations; while selective association, which is known to be general

among distinct varieties or breeds of the same species, will produce an

effective isolation even when the two forms occupy the same area.

From the various considerations now adverted to, Mr. Darwin arrived at

the conclusion that the sterility or infertility of species with each

other, whether manifested in the difficulty of obtaining first crosses

between them or in the sterility of the hybrids thus obtained, is not a

constant or necessary result of specific difference, but is incidental

on unknown peculiarities of the reproductive system. These peculiarities

constantly tend to arise under changed conditions owing to the extreme

susceptibility of that system, and they are usually correlated with

variations of form or of colour. Hence, as fixed differences of form and

colour, slowly gained by natural selection in adaptation to changed

conditions, are what essentially characterise distinct species, some

amount of infertility between species is the usual result.

Here the problem was left by Mr. Darwin; but we have shown that its

solution may be carried a step further. If we accept the association of

some degree of infertility, however slight, as a not unfrequent

accompaniment of the external differences which always arise in a state

of nature between varieties and incipient species, it has been shown

that natural selection \_has\_ power to increase that infertility just as

it has power to increase other favourable variations. Such an increase

of infertility will be beneficial, whenever new species arise in the

same area with the parent form; and we thus see how, out of the

fluctuating and very unequal amounts of infertility correlated with

physical variations, there may have arisen that larger and more constant

amount which appears usually to characterise well-marked species.

The great body of facts of which a condensed account has been given in

the present chapter, although from an experimental point of view very

insufficient, all point to the general conclusion we have now reached,

and afford us a not unsatisfactory solution of the great problem of

hybridism in relation to the origin of species by means of natural

selection. Further experimental research is needed in order to complete

the elucidation of the subject; but until these additional facts are

forthcoming no new theory seems required for the explanation of the

phenomena.

FOOTNOTES:

[Footnote 51: Darwin's \_Animals and Plants under Domestication\_, vol.

ii. pp. 163-170.]

[Footnote 52: For a full account of these interesting facts and of the

various problems to which they give rise, the reader must consult

Darwin's volume on \_The Different Forms of Flowers in Plants of the same

Species\_, chaps, i.-iv.]

[Footnote 53: See \_Nature\_, vol. xxi. p. 207.]

[Footnote 54: Low's \_Domesticated Animals of Great Britain\_,

Introduction, p. lxiv.]

[Footnote 55: Low's \_Domesticated Animals\_, p. 28.]

[Footnote 56: \_Amaryllidaceae\_, by the Hon. and Rev. William Herbert, p.

379.]

[Footnote 57: \_Origin of Species\_, p. 239.]

[Footnote 58: \_Origin of Species\_, sixth edition, p. 9.]

[Footnote 59: In the \_Medico-Chirurgical Transactions\_, vol. liii.

(1870), Dr. Ogle has adduced some curious physiological facts bearing on

the presence or absence of white colours in the higher animals. He

states that a dark pigment in the olfactory region of the nostrils is

essential to perfect smell, and that this pigment is rarely deficient

except when the whole animal is pure white, and the creature is then

almost without smell or taste. He observes that there is no proof that,

in any of the cases given above, the black animals actually eat the

poisonous root or plant; and that the facts are readily understood if

the senses of smell and taste are dependent on a pigment which is absent

in the white animals, who therefore eat what those gifted with normal

senses avoid. This explanation however hardly seems to cover the facts.

We cannot suppose that almost all the sheep in the world (which are

mostly white) are without smell or taste. The cutaneous disease on the

white patches of hair on horses, the special liability of white terriers

to distemper, of white chickens to the gapes, and of silkworms which

produce yellow silk to the fungus, are not explained by it. The

analogous facts in plants also indicate a real constitutional relation

with colour, not an affection of the sense of smell and taste only.]

[Footnote 60: For all these facts, see \_Animals and Plants under

Domestication\_, vol. ii. pp. 335-338.]

[Footnote 61: \_Animals and Plants under Domestication\_, vol. ii. pp.

102, 103.]

[Footnote 62: As this argument is a rather difficult one to follow,

while its theoretical importance is very great, I add here the following

briefer exposition of it, in a series of propositions; being, with a few

verbal alterations, a copy of what I wrote on the subject about twenty

years back. Some readers may find this easier to follow than the fuller

discussion in the text:--

\_Can Sterility of Hybrids have been Produced by Natural

Selection?\_

1. Let there be a species which has varied into \_two forms\_ each

adapted to certain existing conditions better than the parent

form, which they soon supplant.

2. If these \_two forms\_, which are supposed to coexist in the

same district, do not intercross, natural selection will

accumulate all favourable variations till they become well

suited to their conditions of life, and form two slightly

differing species.

3. But if these \_two forms\_ freely intercross with each other,

and produce hybrids, which are also quite fertile \_inter se\_,

then the formation of the two distinct races or species will be

retarded, or perhaps entirely prevented; for the offspring of

the crossed unions will be \_more vigorous\_ owing to the cross,

although \_less adapted\_ to their conditions of life than either

of the pure breeds.

4. Now, let a partial sterility of the hybrids of some

considerable proportion of these two forms arise; and, as this

would probably be due to some special conditions of life, we may

fairly suppose it to arise in some definite portion of the area

occupied by the two forms.

5. The result will be that, in that area, the hybrids (although

continually produced by first crosses almost as freely as

before) will not themselves increase so rapidly as the two pure

forms; and as the two pure forms are, by the terms of the

problem, better suited to their several conditions of life than

the hybrids, they will inevitably increase more rapidly, and

will continually tend to supplant the hybrids altogether at

every recurrent severe struggle for existence.

6. We may fairly suppose, also, that as soon as any sterility

appears some disinclination to \_cross unions\_ will appear, and

this will further tend to the diminution of the production of

hybrids.

7. In the other part of the area, however, where hybridism

occurs with perfect freedom, hybrids of various degrees may

increase till they equal or even exceed in number the pure

species--that is, the incipient species will be liable to be

swamped by intercrossing.

8. The first result, then, of a partial sterility of crosses

appearing in one part of the area occupied by the two forms,

will be--that the great majority of the individuals will there

consist of the two pure forms only, while in the remaining part

these will be in a minority,--which is the same as saying that

the new \_physiological variety\_ of the two forms will be better

suited to the conditions of existence than the remaining portion

which has not varied physiologically.

9. But when the struggle for existence becomes severe, that

variety which is best adapted to the conditions of existence

always supplants that which is imperfectly adapted; therefore,

\_by natural selection\_ the \_varieties\_ which are \_sterile\_ when

crossed will become established as the only ones.

10. Now let variations in the \_amount of sterility\_ and in

the \_disinclination to crossed unions\_ continue to occur--also

in certain parts of the area: exactly the same result must

recur, and the progeny of this new physiological variety will in

time occupy the whole area.

11. There is yet another consideration that would facilitate the

process. It seems probable that the \_sterility variations\_

would, to some extent, concur with, and perhaps depend upon, the

\_specific variations\_; so that, just in proportion as the \_two

forms\_ diverged and became better adapted to the conditions of

existence, they would become more sterile when intercrossed. If

this were the case, then natural selection would act with double

strength; and those which were better adapted to survive both

structurally and physiologically would certainly do so.]

[Footnote 63: Cases of this kind are referred to at p. 155. It must,

however, be noted, that such sterility in first crosses appears to be

equally rare between different species of the same genus as between

individuals of the same species. Mules and other hybrids are freely

produced between very distinct species, but are themselves infertile or

quite sterile; and it is this infertility or sterility of the hybrids

that is the characteristic--and was once thought to be the criterion--of

species, not the sterility of their first crosses. Hence we should not

expect to find any constant infertility in the first crosses between the

distinct strains or varieties that formed the starting-point of new

species, but only a slight amount of infertility in their mongrel

offspring. It follows, that Mr. Romanes' theory of \_Physiological

Selection\_--which assumes sterility or infertility between first crosses

as the fundamental fact in the origin of species--does not accord with

the general phenomena of hybridism in nature.]

[Footnote 64: The exact number is 1219.51, but the fractions are omitted

for clearness.]

CHAPTER VIII

THE ORIGIN AND USES OF COLOUR IN ANIMALS

The Darwinian theory threw new light on organic colour--The

problem to be solved--The constancy of animal colour indicates

utility--Colour and environment--Arctic animals

white--Exceptions prove the rule--Desert, forest, nocturnal, and

oceanic animals--General theories of animal colour--Variable

protective colouring--Mr. Poulton's experiments--Special or

local colour adaptations--Imitation of particular objects--How

they have been produced--Special protective colouring of

butterflies--Protective resemblance among marine

animals--Protection by terrifying enemies--Alluring

coloration--The coloration of birds' eggs--Colour as a means of

recognition--Summary of the preceding exposition--Influence of

locality or of climate on colour--Concluding remarks.

Among the numerous applications of the Darwinian theory in the

interpretation of the complex phenomena presented by the organic world,

none have been more successful, or are more interesting, than those

which deal with the colours of animals and plants. To the older school

of naturalists colour was a trivial character, eminently unstable and

untrustworthy in the determination of species; and it appeared to have,

in most cases, no use or meaning to the objects which displayed it. The

bright and often gorgeous coloration of insect, bird, or flower, was

either looked upon as having been created for the enjoyment of mankind,

or as due to unknown and perhaps undiscoverable laws of nature.

But the researches of Mr. Darwin totally changed our point of view in

this matter. He showed, clearly, that some of the colours of animals are

useful, some hurtful to them; and he believed that many of the most

brilliant colours were developed by sexual choice; while his great

general principle, that all the fixed characters of organic beings have

been developed under the action of the law of utility, led to the

inevitable conclusion that so remarkable and conspicuous a character as

colour, which so often constitutes the most obvious distinction of

species from species, or group from group, must also have arisen from

survival of the fittest, and must, therefore, in most cases have some

relation to the wellbeing of its possessors. Continuous observation and

research, carried on by multitudes of observers during the last thirty

years, have shown this to be the case; but the problem is found to be

far more complex than was at first supposed. The modes in which colour

is of use to different classes of organisms is very varied, and have

probably not yet been all discovered; while the infinite variety and

marvellous beauty of some of its developments are such as to render it

hopeless to arrive at a complete and satisfactory explanation of every

individual case. So much, however, has been achieved, so many curious

facts have been explained, and so much light has been thrown on some of

the most obscure phenomena of nature, that the subject deserves a

prominent place in any account of the Darwinian theory.

\_The Problem to be Solved.\_

Before dealing with the various modifications of colour in the animal

world it is necessary to say a few words on colour in general, on its

prevalence in nature, and how it is that the colours of animals and

plants require any special explanation. What we term colour is a

subjective phenomenon, due to the constitution of our mind and nervous

system; while, objectively, it consists of light-vibrations of different

wave-lengths emitted by, or reflected from, various objects. Every

visible object must be coloured, because to be visible it must send rays

of light to our eye. The kind of light it sends is modified by the

molecular constitution or the surface texture of the object. Pigments

absorb certain rays and reflect the remainder, and this reflected

portion has to our eyes a definite colour, according to the portion of

the rays constituting white light which are absorbed. Interference

colours are produced either by thin films or by very fine striae on the

surfaces of bodies, which cause rays of certain wave-lengths to

neutralise each other, leaving the remainder to produce the effects of

colour. Such are the colours of soap-bubbles, or of steel or glass on

which extremely fine lines have been ruled; and these colours often

produce the effect of metallic lustre, and are the cause of most of the

metallic hues of birds and insects.

As colour thus depends on molecular or chemical constitution or on the

minute surface texture of bodies, and, as the matter of which organic

beings are composed consists of chemical compounds of great complexity

and extreme instability, and is also subject to innumerable changes

during growth and development, we might naturally expect the phenomena

of colour to be more varied here than in less complex and more stable

compounds. Yet even in the inorganic world we find abundant and varied

colours; in the earth and in the water; in metals, gems, and minerals;

in the sky and in the ocean; in sunset clouds and in the many-tinted

rainbow. Here we can have no question of \_use\_ to the coloured object,

and almost as little perhaps in the vivid red of blood, in the brilliant

colours of red snow and other low algae and fungi, or even in the

universal mantle of green which clothes so large a portion of the

earth's surface. The presence of some colour, or even of many brilliant

colours, in animals and plants would require no other explanation than

does that of the sky or the ocean, of the ruby or the emerald--that is,

it would require a purely physical explanation only. It is the wonderful

individuality of the colours of animals and plants that attracts our

attention--the fact that the colours are localised in definite patterns,

sometimes in accordance with structural characters, sometimes altogether

independent of them; while often differing in the most striking and

fantastic manner in allied species. We are thus compelled to look upon

colour not merely as a physical but also as a biological characteristic,

which has been differentiated and specialised by natural selection, and

must, therefore, find its explanation in the principle of adaptation or

utility.

\_The Constancy of Animal Colour indicates Utility.\_

That the colours and markings of animals have been acquired under the

fundamental law of utility is indicated by a general fact which has

received very little attention. As a rule, colour and marking are

constant in each species of wild animal, while, in almost every

domesticated animal, there arises great variability. We see this in our

horses and cattle, our dogs and cats, our pigeons and poultry. Now, the

essential difference between the conditions of life of domesticated and

wild animals is, that the former are protected by man, while the latter

have to protect themselves. The extreme variations in colour that

immediately arise under domestication indicate a tendency to vary in

this way, and the occasional occurrence of white or piebald or other

exceptionally coloured individuals of many species in a state of nature,

shows that this tendency exists there also; and, as these exceptionally

coloured individuals rarely or never increase, there must be some

constant power at work to keep it in check. This power can only be

natural selection or the survival of the fittest, which again implies

that some colours are useful, some injurious, in each particular case.

With this principle as our guide, let us see how far we can account both

for the general and special colours of the animal world.

\_Colour and Environment.\_

The fact that first strikes us in our examination of the colours of

animals as a whole, is the close relation that exists between these

colours and the general environment. Thus, white prevails among arctic

animals; yellow or brown in desert species; while green is only a common

colour in tropical evergreen forests. If we consider these cases

somewhat carefully we shall find, that they afford us excellent

materials for forming a judgment on the various theories that have been

suggested to account for the colours of the animal world.

In the arctic regions there are a number of animals which are wholly

white all the year round, or which only turn white in winter. Among the

former are the polar bear and the American polar hare, the snowy owl and

the Greenland falcon; among the latter the arctic fox, the arctic hare,

the ermine, and the ptarmigan. Those which are permanently white remain

among the snow nearly all the year round, while those which change their

colour inhabit regions which are free from snow in summer. The obvious

explanation of this style of coloration is, that it is protective,

serving to conceal the herbivorous species from their enemies, and

enabling carnivorous animals to approach their prey unperceived. Two

other explanations have, however, been suggested. One is, that the

prevalent white of the arctic regions has a direct effect in producing

the white colour in animals, either by some photographic or chemical

action on the skin or by a reflex action through vision. The other is,

that the white colour is chiefly beneficial as a means of checking

radiation and so preserving animal heat during the severity of an arctic

winter. The first is part of the general theory that colour is the

effect of coloured light on the objects--a pure hypothesis which has, I

believe, no facts whatever to support it. The second suggestion is also

an hypothesis merely, since it has not been proved by experiment that a

white colour, \_per se\_, independently of the fur or feathers which is so

coloured, has any effect whatever in checking the radiation of low-grade

heat like that of the animal body. But both alike are sufficiently

disproved by the interesting exceptions to the rule of white coloration

in the arctic regions, which exceptions are, nevertheless, quite in

harmony with the theory of protection.

Whenever we find arctic animals which, from whatever cause, do not

require protection by the white colour, then neither the cold nor the

snow-glare has any effect upon their coloration. The sable retains its

rich brown fur throughout the Siberian winter; but it frequents trees at

that season and not only feeds partially on fruits or seeds, but is able

to catch birds among the branches of the fir-trees, with the bark of

which its colour assimilates. Then we have that thoroughly arctic

animal, the musk-sheep, which is brown and conspicuous; but this animal

is gregarious, and its safety depends on its association in small herds.

It is, therefore, of more importance for it to be able to recognise its

kind at a distance than to be concealed from its enemies, against which

it can well protect itself so long as it keeps together in a compact

body. But the most striking example is that of the common raven, which

is a true arctic bird, and is found even in mid-winter as far north as

any known bird or mammal. Yet it always retains its black coat, and the

reason, from our point of view, is obvious. The raven is a powerful bird

and fears no enemy, while, being a carrion-feeder, it has no need for

concealment in order to approach its prey. The colour of the raven and

of the musk-sheep are, therefore, both inconsistent with any other

theory than that the white colour of arctic animals has been acquired

for concealment, and to that theory both afford a strong support. Here

we have a striking example of the exception proving the rule.

In the desert regions of the earth we find an even more general

accordance of colour with surroundings. The lion, the camel, and all the

desert antelopes have more or less the colour of the sand or rock among

which they live. The Egyptian cat and the Pampas cat are sandy or earth

coloured. The Australian kangaroos are of similar tints, and the

original colour of the wild horse is supposed to have been sandy or clay

coloured. Birds are equally well protected by assimilative hues; the

larks, quails, goatsuckers, and grouse which abound in the North African

and Asiatic deserts are all tinted or mottled so as closely to resemble

the average colour of the soil in the districts they inhabit. Canon

Tristram, who knows these regions and their natural history so well,

says, in an often quoted passage: "In the desert, where neither trees,

brushwood, nor even undulations 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."

Passing on to the tropical regions, it is among their evergreen forests

alone that we find whole groups of birds whose ground colour is green.

Parrots are very generally green, and in the East we have an extensive

group of green fruit-eating pigeons; while the barbets, bee-eaters,

turacos, leaf-thrushes (Phyllornis), white-eyes (Zosterops), and many

other groups, have so much green in their plumage as to tend greatly to

their concealment among the dense foliage. There can be no doubt that

these colours have been acquired as a protection, when we see that in

all the temperate regions, where the leaves are deciduous, the ground

colour of the great majority of birds, especially on the upper surface,

is a rusty brown of various shades, well corresponding with the bark,

withered leaves, ferns, and bare thickets among which they live in

autumn and winter, and especially in early spring when so many of them

build their nests.

Nocturnal animals supply another illustration of the same rule, in the

dusky colours of mice, rats, bats, and moles, and in the soft mottled

plumage of owls and goatsuckers which, while almost equally

inconspicuous in the twilight, are such as to favour their concealment

in the daytime.

An additional illustration of general assimilation of colour to the

surroundings of animals, is furnished by the inhabitants of the deep

oceans. Professor Moseley of the Challenger Expedition, in his British

Association lecture on this subject, says: "Most characteristic of

pelagic animals is the almost crystalline transparency of their bodies.

So perfect is this transparency that very many of them are rendered

almost entirely invisible when floating in the water, while some, even

when caught and held up in a glass globe, are hardly to be seen. The

skin, nerves, muscles, and other organs are absolutely hyaline and

transparent, but the liver and digestive tract often remain opaque and

of a yellow or brown colour, and exactly resemble when seen in the water

small pieces of floating seaweed." Such marine organisms, however, as

are of larger size, and either occasionally or habitually float on the

surface, are beautifully tinged with blue above, thus harmonising with

the colour of the sea as seen by hovering birds; while they are white

below, and are thus invisible against the wave-foam and clouds as seen

by enemies beneath the surface. Such are the tints of the beautiful

nudibranchiate mollusc, Glaucus atlanticus, and many others.

\_General Theories of Animal Colour.\_

We are now in a position to test the general theories, or, to speak more

correctly, the popular notions, as to the origin of animal coloration,

before proceeding to apply the principle of utility to the explanation

of some among the many extraordinary manifestations of colour in the

animal world. The most generally received theory undoubtedly is, that

brilliancy and variety of colour are due to the direct action of light

and heat; a theory no doubt derived from the abundance of

bright-coloured birds, insects, and flowers which are brought from

tropical regions. There are, however, two strong arguments against this

theory. We have already seen how generally bright coloration is wanting

in desert animals, yet here heat and light are both at a maximum, and if

these alone were the agents in the production of colour, desert animals

should be the most brilliant. Again, all naturalists who have lived in

tropical regions know that the proportion of bright to dull coloured

species is little if any greater there than in the temperate zone, while

there are many tropical groups in which bright colours are almost

entirely unknown. No part of the world presents so many brilliant birds

as South America, yet there are extensive families, containing many

hundreds of species, which are as plainly coloured as our average

temperate birds. Such are the families of the bush-shrikes and

ant-thrushes (Formicariidae), the tyrant-shrikes (Tyrannidae), the

American creepers (Dendrocolaptidae), together with a large proportion

of the wood-warblers (Mniotiltidae), the finches, the wrens, and some

other groups. In the eastern hemisphere, also, we have the

babbling-thrushes (Timaliidae), the cuckoo-shrikes (Campephagidae), the

honey-suckers (Meliphagidae), and several other smaller groups which are

certainly not coloured above the average standard of temperate birds.

Again, there are many families of birds which spread over the whole

world, temperate and tropical, and among these the tropical species

rarely present any exceptional brilliancy of colour. Such are the

thrushes, goatsuckers, hawks, plovers, and ducks; and in the last-named

group it is the temperate and arctic zones that afford the most

brilliant coloration.

The same general facts are found to prevail among insects. Although

tropical insects present some of the most gorgeous coloration in the

whole realm of nature, yet there are thousands and tens of thousands of

species which are as dull coloured as any in our cloudy land. The

extensive family of the carnivorous ground-beetles (Carabidae) attains

its greatest brilliancy in the temperate zone; while by far the larger

proportion of the great families of the longicorns and the weevils, are

of obscure colours even in the tropics. In butterflies, there is

undoubtedly a larger proportion of brilliant colour in the tropics; but

if we compare families which are almost equally developed over the

globe--as the Pieridae or whites and yellows, and the Satyridae or

ringlets--we shall find no great disproportion in colour between those

of temperate and tropical regions.

The various facts which have now briefly been noticed are sufficient to

indicate that the light and heat of the sun are not the direct causes of

the colours of animals, although they may favour the production of

colour when, as in tropical regions, the persistent high temperature

favours the development of the maximum of life. We will now consider the

next suggestion, that light reflected from surrounding coloured objects

tends to produce corresponding colours in the animal world.

This theory is founded on a number of very curious facts which prove,

that such a change does sometimes occur and is directly dependent on the

colours of surrounding objects; but these facts are comparatively rare

and exceptional in their nature, and the same theory will certainly not

apply to the infinitely varied colours of the higher animals, many of

which are exposed to a constantly varying amount of light and colour

during their active existence. A brief sketch of these dependent changes

of colour may, however, be advantageously given here.

\_Variable Protective Colouring.\_

There are two distinct kinds of change of colour in animals due to the

colouring of the environment. In one case the change is caused by reflex

action set up by the animal \_seeing\_ the colour to be imitated, and the

change produced can be altered or repeated as the animal changes its

position. In the other case the change occurs but once, and is probably

not due to any conscious or sense action, but to some direct influence

on the surface tissues while the creature is undergoing a moult or

change to the pupa form.

The most striking example of the first class is that of the chameleon,

which changes to white, brown, yellowish, or green, according to the

colour of the object on which it rests. This change is brought about by

means of two layers of pigment cells, deeply seated in the skin, and of

bluish and yellowish colours. By suitable muscles these cells can be

forced upwards so as to modify the colour of the skin, which, when they

are not brought into action, is a dirty white. These animals are

excessively sluggish and defenceless, and the power of changing their

colour to that of their immediate surroundings is no doubt of great

service to them. Many of the flatfish are also capable of changing their

colour according to the colour of the bottom they rest on; and frogs

have a similar power to a limited extent. Some crustacea also change

colour, and the power is much developed in the Chameleon shrimp (Mysis

Chamaeleon) which is gray when on sand, but brown or green when among

brown or green seaweed. It has been proved by experiment that when this

animal is blinded the change does not occur. In all these cases,

therefore, we have some form of reflex or sense action by which the

change is produced, probably by means of pigment cells beneath the skin

as in the chameleon.

The second class consists of certain larvae, and pupae, which undergo

changes of colour when exposed to differently coloured surroundings.

This subject has been carefully investigated by Mr. E.B. Poulton, who

has communicated the results of his experiments to the Royal

Society.[65] It had been noticed that some species of larvae which fed

on several different plants had colours more or less corresponding to

the particular plant the individual fed on. Numerous cases are given in

Professor Meldola's article on "Variable Protective Colouring" (\_Proc.

Zool. Soc.\_, 1873, p. 153), and while the general green coloration was

attributed to the presence of chlorophyll beneath the skin, the

particular change in correspondence to each food-plant was attributed to

a special function which had been developed by natural selection. Later

on, in a note to his translation of Weissmann's \_Theory of Descent\_,

Professor Meldola seemed disposed to think that the variations of colour

of some of the species might be phytophagic--that is, due to the direct

action of the differently coloured leaves on which the insect fed. Mr.

Poulton's experiments have thrown much light on this question, since he

has conclusively proved that, in the case of the sphinx caterpillar of

Smerinthus ocellatus, the change of colour is not due to the food but to

the coloured light reflected from the leaves.

This was shown by feeding two sets of larvae on the same plant but

exposed to differently coloured surroundings, obtained by sewing the

leaves together, so that in one case only the dark upper surface, in the

other the whitish under surface was exposed to view. The result in each

case was a corresponding change of colour in the larvae, confirming the

experiments on different individuals of the same batch of larvae which

had been supplied with different food-plants or exposed to a different

coloured light.

An even more interesting series of experiments was made on the colours

of pupae, which in many cases were known to be affected by the material

on which they underwent their transformations. The late Mr. T.W. Wood

proved, in 1867, that the pupae of the common cabbage butterflies

(Pieris brassicae and P. rapae) were either light, or dark, or green,

according to the coloured boxes they were kept in, or the colours of the

fences, walls, etc., against which they were suspended. Mrs. Barber in

South Africa found that the pupae of Papilio Nireus underwent a similar

change, being deep green when attached to orange leaves of the same

tint, pale yellowish-green when on a branch of the bottle-brush tree

whose half-dried leaves were of this colour, and yellowish when attached

to the wooden frame of a box. A few other observers noted similar

phenomena, but nothing more was done till Mr. Poulton's elaborate series

of experiments with the larvae of several of our common butterflies were

the means of clearing up several important points. He showed that the

action of the coloured light did not affect the pupa itself but the

larva, and that only for a limited period of time. After a caterpillar

has done feeding it wanders about seeking a suitable place to undergo

its transformation. When this is found it rests quietly for a day or

two, spinning the web from which it is to suspend itself; and it is

during this period of quiescence, and perhaps also the first hour or two

after its suspension, that the action of the surrounding coloured

surfaces determines, to a considerable extent, the colour of the pupa.

By the application of various surrounding colours during this period,

Mr. Poulton was able to modify the colour of the pupa of the common

tortoise-shell butterfly from nearly black to pale, or to a brilliant

golden; and that of Pieris rapae from dusky through pinkish to pale

green. It is interesting to note, that the colours produced were in all

cases such only as assimilated with the surroundings usually occupied by

the species, and also, that colours which did not occur in such

surroundings, as dark red or blue, only produced the same effects as

dusky or black.

Careful experiments were made to ascertain whether the effect was

produced through the sight of the caterpillar. The ocelli were covered

with black varnish, but neither this, nor cutting off the spines of the

tortoise-shell larva to ascertain whether they might be sense-organs,

produced any effect on the resulting colour. Mr. Poulton concludes,

therefore, that the colour-action probably occurs over the whole surface

of the body, setting up physiological processes which result in the

corresponding colour-change of the pupa. Such changes are, however, by

no means universal, or even common, in protectively coloured pupae,

since in Papilio machaon and some others which have been experimented

on, both in this country and abroad, no change can be produced on the

pupa by any amount of exposure to differently coloured surroundings. It

is a curious point that, with the small tortoise-shell larva, exposure

to light from gilded surfaces produced pupae with a brilliant golden

lustre; and the explanation is supposed to be that mica abounded in the

original habitat of the species, and that the pupae thus obtained

protection when suspended against micaceous rock. Looking, however, at

the wide range of the species and the comparatively limited area in

which micaceous rocks occur, this seems a rather improbable explanation,

and the occurrence of this metallic appearance is still a difficulty. It

does not, however, commonly occur in this country in a natural state.

The two classes of variable colouring here discussed are evidently

exceptional, and can have little if any relation to the colours of those

more active creatures which are continually changing their position with

regard to surrounding objects, and whose colours and markings are nearly

constant throughout the life of the individual, and (with the exception

of sexual differences) in all the individuals of the species. We will

now briefly pass in review the various characteristics and uses of the

colours which more generally prevail in nature; and having already

discussed those protective colours which serve to harmonise animals with

their general environment, we have to consider only those cases in which

the colour resemblance is more local or special in its character.

\_Special or Local Colour Adaptations.\_

This form of colour adaptation is generally manifested by markings

rather than by colour alone, and is extremely prevalent both among

insects and vertebrates, so that we shall be able to notice only a few

illustrative cases. Among our native birds we have the snipe and

woodcock, whose markings and tints strikingly accord with the dead marsh

vegetation among which they live; the ptarmigan in its summer dress is

mottled and tinted exactly like the lichens which cover the stones of

the higher mountains; while young unfledged plovers are spotted so as

exactly to resemble the beach pebbles among which they crouch for

protection, as beautifully exhibited in one of the cases of British

birds in the Natural History Museum at South Kensington.

In mammalia, we notice the frequency of rounded spots on forest or tree

haunting animals of large size, as the forest deer and the forest cats;

while those that frequent reedy or grassy places are striped vertically,

as the marsh antelopes and the tiger. I had long been of opinion that

the brilliant yellow and black stripes of the tiger were adaptive, but

have only recently obtained proof that it is so. An experienced

tiger-hunter, Major Walford, states in a letter, that the haunts of the

tiger are invariably full of the long grass, dry and pale yellow for at

least nine months of the year, which covers the ground wherever there is

water in the rainy season, and he adds: "I once, while following up a

wounded tiger, failed for at least a minute to see him under a tree in

grass at a distance of about twenty yards--jungle open--but the natives

saw him, and I eventually made him out well enough to shoot him, but

even then I could not see at what part of him I was aiming. There can be

no doubt whatever that the colour of both the tiger and the panther

renders them almost invisible, especially in a strong blaze of light,

when among grass, and one does not seem to notice stripes or spots till

they are dead." It is the black shadows of the vegetation that

assimilate with the black stripes of the tiger; and, in like manner,

the spotty shadows of leaves in the forest so harmonise with the spots

of ocelots, jaguars, tiger-cats, and spotted deer as to afford them a

very perfect concealment.

In some cases the concealment is effected by colours and markings which

are so striking and peculiar that no one who had not seen the creature

in its native haunts would imagine them to be protective. An example of

this is afforded by the banded fruit pigeon of Timor, whose pure white

head and neck, black wings and back, yellow belly, and deeply-curved

black band across the breast, render it a very handsome and conspicuous

bird. Yet this is what Mr. H.O. Forbes says of it: "On the trees the

white-headed fruit pigeon (Ptilopus cinctus) sate motionless during the

heat of the day in numbers, on well-exposed branches; but it was with

the utmost difficulty that I or my sharp-eyed native servant could ever

detect them, even in trees where we knew they were sitting."[66] The

trees referred to are species of Eucalyptus which abound in Timor. They

have whitish or yellowish bark and very open foliage, and it is the

intense sunlight casting black curved shadows of one branch upon

another, with the white and yellow bark and deep blue sky seen through

openings of the foliage, that produces the peculiar combination of

colours and shadows to which the colours and markings of this bird have

become so closely assimilated.

Even such brilliant and gorgeously coloured birds as the sun-birds of

Africa are, according to an excellent observer, often protectively

coloured. Mrs. M.E. Barber remarks that "A casual observer would

scarcely imagine that the highly varnished and magnificently coloured

plumage of the various species of Noctarinea could be of service to

them, yet this is undoubtedly the case. The most unguarded moments of

the lives of these birds are those that are spent amongst the flowers,

and it is then that they are less wary than at any other time. The

different species of aloes, which blossom in succession, form the

principal sources of their winter supplies of food; and a legion of

other gay flowering plants in spring and summer, the aloe blossoms

especially, are all brilliantly coloured, and they harmonise admirably

with the gay plumage of the different species of sun-birds. Even the

keen eye of a hawk will fail to detect them, so closely do they resemble

the flowers they frequent. The sun-birds are fully aware of this fact,

for no sooner have they relinquished the flowers than they become

exceedingly wary and rapid in flight, darting arrow-like through the air

and seldom remaining in exposed situations. The black sun-bird

(Nectarinea amethystina) is never absent from that magnificent

forest-tree, the 'Kaffir Boom' (Erythrina caffra); all day long the

cheerful notes of these birds may be heard amongst its spreading

branches, yet the general aspect of the tree, which consists of a huge

mass of scarlet and purple-black blossoms without a single green leaf,

blends and harmonises with the colours of the black sun-bird to such an

extent that a dozen of them may be feeding amongst its blossoms without

being conspicuous, or even visible."[67]

Some other cases will still further illustrate how the colours of even

very conspicuous animals may be adapted to their peculiar haunts.

The late Mr. Swinhoe says of the Kerivoula picta, which he observed in

Formosa: "The body of this bat was of an orange colour, but the wings

were painted with orange-yellow and black. It was caught suspended, head

downwards, on a cluster of the fruit of the longan tree (Nephelium

longanum). Now this tree is an evergreen, and all the year round some

portion of its foliage is undergoing decay, the particular leaves being,

in such a stage, partially orange and black. This bat can, therefore, at

all seasons suspend from its branches and elude its enemies by its

resemblance to the leaves of the tree."[68]

Even more curious is the case of the sloths--defenceless animals which

feed upon leaves, and hang from the branches of trees with their back

downwards. Most of the species have a curious buff-coloured spot on the

back, rounded or oval in shape and often with a darker border, which

seems placed there on purpose to make them conspicuous; and this was a

great puzzle to naturalists, because the long coarse gray or greenish

hair was evidently like tree-moss and therefore protective. But an old

writer, Baron von Slack, in his \_Voyage\_ \_to Surinam\_ (1810), had

already explained the matter. He says: "The colour and even the shape of

the hair are much like withered moss, and serve to hide the animal in

the trees, but particularly when it has that orange-coloured spot

between the shoulders and lies close to the tree; it looks then exactly

like a piece of branch where the rest has been broken off, by which the

hunters are often deceived." Even such a huge animal as the giraffe is

said to be perfectly concealed by its colour and form when standing

among the dead and broken trees that so often occur on the outskirts of

the thickets where it feeds. The large blotch-like spots on the skin and

the strange shape of the head and horns, like broken branches, so tend

to its concealment that even the keen-eyed natives have been known to

mistake trees for giraffes or giraffes for trees.

Innumerable examples of this kind of protective colouring occur among

insects; beetles mottled like the bark of trees or resembling the sand

or rock or moss on which they live, with green caterpillars of the exact

general tints of the foliage they feed on; but there are also many cases

of detailed imitation of particular objects by insects that must be

briefly described.[69]

\_Protective Imitation of Particular Objects.\_

The insects which present this kind of imitation most perfectly are the

Phasmidae, or stick and leaf insects. The well-known leaf-insects of

Ceylon and of Java, species of Phyllium, are so wonderfully coloured and

veined, with leafy expansions on the legs and thorax, that not one

person in ten can see them when resting on the food-plant close beneath

their eyes. Others resemble pieces of stick with all the minutiae of

knots and branches, formed by the insects' legs, which are stuck out

rigidly and unsymmetrically. I have often been unable to distinguish

between one of these insects and a real piece of stick, till I satisfied

myself by touching it and found it to be alive. One species, which was

brought me in Borneo, was covered with delicate semitransparent green

foliations, exactly resembling the hepaticae which cover pieces of

rotten stick in the damp forests. Others resemble dead leaves in all

their varieties of colour and form; and to show how perfect is the

protection obtained and how important it is to the possessors of it, the

following incident, observed by Mr. Belt in Nicaragua, is most

instructive. Describing the armies of foraging ants in the forest which

devour every insect they can catch, he says: "I was much surprised with

the behaviour of a green leaf-like locust. This insect stood immovably

among a host of ants, many of which ran over its legs without ever

discovering there was food within their reach. So fixed was its

instinctive knowledge that its safety depended on its immovability, that

it allowed me to pick it up and replace it among the ants without making

a single effort to escape. This species closely resembles a green

leaf."[70]

Caterpillars also exhibit a considerable amount of detailed resemblance

to the plants on which they live. Grass-feeders are striped

longitudinally, while those on ordinary leaves are always striped

obliquely. Some very beautiful protective resemblances are shown among

the caterpillars figured in Smith and Abbott's \_Lepidopterous Insects of

Georgia\_, a work published in the early part of the century, before any

theories of protection were started. The plates in this work are most

beautifully executed from drawings made by Mr. Abbott, representing the

insects, in every case, on the plants which they frequented, and no

reference is made in the descriptions to the remarkable protective

details which appear upon the plates. We have, first, the larva of

Sphinx fuciformis feeding on a plant with linear grass-like leaves and

small blue flowers; and we find the insect of the same green as the

leaves, striped longitudinally in accordance with the linear leaves, and

with the head blue corresponding both in size and colour with the

flowers. Another species (Sphinx tersa) is represented feeding on a

plant with small red flowers situated in the axils of the leaves; and

the larva has a row of seven red spots, unequal in size, and

corresponding very closely with the colour and size of the flowers. Two

other figures of sphinx larvae are very curious. That of Sphinx

pampinatrix feeds on a wild vine (Vitis indivisa), having green

tendrils, and in this species the curved horn on the tail is green, and

closely imitates in its curve the tip of the tendril. But in another

species (Sphinx cranta), which feeds on the fox-grape (Vitis vulpina),

the horn is very long and red, corresponding with the long red-tipped

tendrils of the plant. Both these larvae are green with oblique stripes,

to harmonise with the veined leaves of the vines; but a figure is also

given of the last-named species after it has done feeding, when it is of

a decided brown colour and has entirely lost its horn. This is because

it then descends to the ground to bury itself, and the green colour and

red horn would be conspicuous and dangerous; it therefore loses both at

the last moult. Such a change of colour occurs in many species of

caterpillars. Sometimes the change is seasonal; and, in those which

hibernate with us, the colour of some species, which is brownish in

autumn in adaptation to the fading foliage, becomes green in spring to

harmonise with the newly-opened leaves at that season.[71]

Some of the most curious examples of minute imitation are afforded by

the caterpillars of the geometer moths, which are always brown or

reddish, and resemble in form little twigs of the plant on which they

feed. They have the habit, when at rest, of standing out obliquely from

the branch, to which they hold on by their hind pair of prolegs or

claspers, and remain motionless for hours. Speaking of these protective

resemblances Mr. Jenner Weir says: "After being thirty years an

entomologist I was deceived myself, and took out my pruning scissors to

cut from a plum tree a spur which I thought I had overlooked. This

turned out to be the larva of a geometer two inches long. I showed it

to several members of my family, and defined a space of four inches in

which it was to be seen, but none of them could perceive that it was a

caterpillar."[72]

One more example of a protected caterpillar must be given. Mr. A.

Everett, writing from Sarawak, Borneo, says: "I had a caterpillar

brought me, which, being mixed by my boy with some other things, I took

to be a bit of moss with two exquisite pinky-white seed-capsules; but I

soon saw that it moved, and examining it more closely found out its real

character: it is covered with hair, with two little pink spots on the

upper surface, the general hue being more green. Its motions are very

slow, and when eating the head is withdrawn beneath a fleshy mobile

hood, so that the action of feeding does not produce any movement

externally. It was found in the limestone hills at Busan, the situation

of all others where mosses are most plentiful and delicate, and where

they partially clothe most of the protruding masses of rock."

\_How these Imitations have been Produced.\_

To many persons it will seem impossible that such beautiful and detailed

resemblances as those now described--and these are only samples of

thousands that occur in all parts of the world--can have been brought

about by the preservation of accidental useful variations. But this will

not seem so surprising if we keep in mind the facts set forth in our

earlier chapters--the rapid multiplication, the severe struggle for

existence, and the constant variability of these and all other

organisms. And, further, we must remember that these delicate

adjustments are the result of a process which has been going on for

millions of years, and that we now see the small percentage of successes

among the myriads of failures. From the very first appearance of insects

and their various kinds of enemies the need of protection arose, and was

usually most easily met by modifications of colour. Hence, we may be

sure that the earliest leaf-eating insects acquired a green colour as

one of the necessities of their existence; and, as the species became

modified and specialised, those feeding on particular species of plants

would rapidly acquire the peculiar tints and markings best adapted to

conceal them upon those plants. Then, every little variation that, once

in a hundred years perhaps, led to the preservation of some larva which

was thereby rather better concealed than its fellows, would form the

starting-point of a further development, leading ultimately to that

perfection of imitation in details which now astonishes us. The

researches of Dr. Weismann illustrate this progressive adaptation. The

very young larvae of several species are green or yellowish without any

markings; they then, in subsequent moults, obtain certain markings, some

of which are often lost again before the larva is fully grown. The early

stages of those species which, like elephant hawk-moths (Chaerocampa),

have the anterior segments elongated and retractile, with large eye-like

spots to imitate the head of a vertebrate, are at first like those of

non-retractile species, the anterior segments being as large as the

rest. After the first moult they become smaller, comparatively; but it

is only after the second moult that the ocelli begin to appear, and

these are not fully defined till after the third moult. This progressive

development of the individual--the ontogeny--gives us a clue to the

ancestral development of the whole race--the phylogeny; and we are

enabled to picture to ourselves the very slow and gradual steps by which

the existing perfect adaptation has been brought about. In many larvae

great variability still exists, and in some there are two or more

distinctly-coloured forms--usually a dark and a light or a brown and a

green form. The larva of the humming-bird hawk-moth (Macroglossa

stellatarum) varies in this manner, and Dr. Weismann raised five

varieties from a batch of eggs from one moth. It feeds on species of

bedstraw (Galium verum and G. mollugo), and as the green forms are less

abundant than the brown, it has probably undergone some recent change of

food-plant or of habits which renders brown the more protective colour.

\_Special Protective Colouring of Butterflies.\_

We will now consider a few cases of special protective colouring in the

perfect butterfly or moth. Mr. Mansel Weale states that in South Africa

there is a great prevalence of white and silvery foliage or bark,

sometimes of dazzling brilliancy, and that many insects and their larvae

have brilliant silvery tints which are protective, among them being

three species of butterflies whose undersides are silvery, and which are

thus effectually protected when at rest.[73] A common African butterfly

(Aterica meleagris) always settles on the ground with closed wings,

which so closely resemble the soil of the district that it can with

difficulty be seen, and the colour varies with the soil in different

localities. Thus specimens from Senegambia were dull brown, the soil

being reddish sand and iron-clay; those from Calabar and Cameroons were

light brown with numerous small white spots, the soil of those countries

being light brown clay with small quartz pebbles; while in other

localities where the colours of the soil were more varied the colours of

the butterfly varied also. Here we have variation in a single species

which has become specialised in certain areas to harmonise with the

colour of the soil.[74]

Many butterflies, in all parts of the world, resemble dead leaves on

their under side, but those in which this form of protection is carried

to the greatest perfection are the species of the Eastern genus Kallima.

In India K. inachis, and in the larger Malay islands K. paralekta, are

very common. They are rather large and showy butterflies, orange and

bluish on the upper side, with a very rapid flight, and frequenting dry

forests. Their habit is to settle always where there is some dead or

decaying foliage, and the shape and colour of the wings (on the under

surface), together with the attitude of the insect, is such as to

produce an absolutely perfect imitation of a dead leaf. This is effected

by the butterfly always settling on a twig, with the short tail of the

hind wings just touching it and forming the leaf-stalk. From this a dark

curved line runs across to the elongated tip of the upper wings,

imitating the midrib, on both sides of which are oblique lines, formed

partly by the nervures and partly by markings, which give the effect of

the usual veining of a leaf. The head and antennae fit exactly between

the closed upper wings so as not to interfere with the outline, which

has just that amount of irregular curvature that is seen in dry and

withered leaves. The colour is very remarkable for its extreme amount of

variability, from deep reddish-brown to olive or pale yellow, hardly two

specimens being exactly alike, but all coming within the range of colour

of leaves in various stages of decay. Still more curious is the fact

that the paler wings, which imitate leaves most decayed, are usually

covered with small black dots, often gathered into circular groups, and

so exactly resembling the minute fungi on decaying leaves that it is

hard at first to believe that the insects themselves are not attacked by

some such fungus. The concealment produced by this wonderful imitation

is most complete, and in Sumatra I have often seen one enter a bush and

then disappear like magic. Once I was so fortunate as to see the exact

spot on which the insect settled; but even then I lost sight of it for

some time, and only after a persistent search discovered that it was

close before my eyes.[75] Here we have a kind of imitation, which is

very common in a less developed form, carried to extreme perfection,

with the result that the species is very abundant over a considerable

area of country.

\_Protective Resemblance among Marine Animals.\_

Among marine animals this form of protection is very common. Professor

Moseley tells us that all the inhabitants of the Gulf-weed are most

remarkably coloured, for purposes of protection and concealment, exactly

like the weed itself. "The shrimps and crabs which swarm in the weed are

of exactly the same shade of yellow as the weed, and have white markings

upon their bodies to represent the patches of Membranipora. The small

fish, Antennarius, is in the same way weed-colour with white spots. Even

a Planarian worm, which lives in the weed, is similarly yellow-coloured,

and also a mollusc, Scyllaea pelagica." The same writer tells us that "a

number of little crabs found clinging to the floats of the blue-shelled

mollusc, Ianthina, were all coloured of a corresponding blue for

concealment."[76]

Professor E.S. Morse of Salem, Mass., found that most of the New

England marine mollusca were protectively coloured; instancing among

others a little red chiton on rocks clothed with red calcareous algae,

and Crepidula plana, living within the apertures of the shells of larger

species of Gasteropods and of a pure white colour corresponding to its

habitat, while allied species living on seaweed or on the outside of

dark shells were dark brown.[77] A still more interesting case has been

recorded by Mr. George Brady. He says: "Amongst the Nullipore which

matted together the laminaria roots in the Firth of Clyde were living

numerous small starfishes (Ophiocoma bellis) which, except when their

writhing movements betrayed them, were quite undistinguishable from the

calcareous branches of the alga; their rigid angularly twisted rays had

all the appearance of the coralline, and exactly assimilated to its dark

purple colour, so that though I held in my hand a root in which were

half a dozen of the starfishes, I was really unable to detect them until

revealed by their movements."[78]

These few examples are sufficient to show that the principle of

protective coloration extends to the ocean as well as over the earth;

and if we consider how completely ignorant we are of the habits and

surroundings of most marine animals, it may well happen that many of the

colours of tropical fishes, which seem to us so strange and so

conspicuous, are really protective, owing to the number of equally

strange and brilliant forms of corals, sea-anemones, sponges, and

seaweeds among which they live.

\_Protection by Terrifying Enemies.\_

A considerable number of quite defenceless insects obtain protection

from some of their enemies by having acquired a resemblance to dangerous

animals, or by some threatening or unusual appearance. This is obtained

either by a modification of shape, of habits, of colour, or of all

combined. The simplest form of this protection is the aggressive

attitude of the caterpillars of the Sphingidae, the forepart of the body

being erected so as to produce a rude resemblance to the figure of a

sphinx, hence the name of the family. The protection is carried further

by those species which retract the first three segments and have large

ocelli on each side of the fourth segment, thus giving to the

caterpillar, when the forepart of its body is elevated, the appearance

of a snake in a threatening attitude.

The blood-red forked tentacle, thrown out of the neck of the larvae of

the genus Papilio when alarmed, is, no doubt, a protection against the

attacks of ichneumons, and may, perhaps, also frighten small birds; and

the habit of turning up the tail possessed by the harmless rove-beetles

(Staphylinidae), giving the idea that they can sting, has, probably, a

similar use. Even an unusual angular form, like a crooked twig or

inorganic substance, may be protective; as Mr. Poulton thinks is the

case with the curious caterpillar of Notodonta ziczac, which, by means

of a few slight protuberances on its body, is able to assume an angular

and very unorganic-looking appearance. But perhaps the most perfect

example of this kind of protection is exhibited by the large caterpillar

of the Royal Persimmon moth (Bombyx regia), a native of the southern

states of North America, and known there as the "Hickory-horned devil."

It is a large green caterpillar, often six inches long, ornamented with

an immense crown of orange-red tubercles, which, if disturbed, it erects

and shakes from side to side in a very alarming manner. In its native

country the negroes believe it to be as deadly as a rattlesnake, whereas

it is perfectly innocuous. The green colour of the body suggests that

its ancestors were once protectively coloured; but, growing too large to

be effectually concealed, it acquired the habit of shaking its head

about in order to frighten away its enemies, and ultimately developed

the crown of tentacles as an addition to its terrifying powers. This

species is beautifully figured in Abbott and Smith's \_Lepidopterous

Insects of Georgia\_.

\_Alluring Coloration.\_

Besides those numerous insects which obtain protection through their

resemblance to the natural objects among which they live, there are some

whose disguise is not used for concealment, but as a direct means of

securing their prey by attracting them within the enemy's reach. Only a

few cases of this kind of coloration have yet been observed, chiefly

among spiders and mantidae; but, no doubt, if attention were given to

the subject in tropical countries, many more would be discovered. Mr.

H.O. Forbes has described a most interesting example of this kind of

simulation in Java. While pursuing a large butterfly through the jungle,

he was stopped by a dense bush, on a leaf of which he observed one of

the skipper butterflies sitting on a bird's dropping. "I had often," he

says, "observed small Blues at rest on similar spots on the ground, and

have wondered what such a refined and beautiful family as the Lycaenidae

could find to enjoy, in food apparently so incongruous for a butterfly.

I approached with gentle steps, but ready net, to see if possible how

the present species was engaged. It permitted me to get quite close, and

even to seize it between my fingers; to my surprise, however, part of

the body remained behind, adhering as I thought to the excreta. I looked

closely, and finally touched with my finger the excreta to find if it

were glutinous. To my delighted astonishment I found that my eyes had

been most perfectly deceived, and that what seemed to be the excreta was

a most artfully coloured spider, lying on its back with its feet crossed

over and closely adpressed to the body." Mr. Forbes then goes on to

describe the exact appearance of such excreta, and how the various parts

of the spider are coloured to produce the imitation, even to the liquid

portion which usually runs a little down the leaf. This is exactly

imitated by a portion of the thin web which the spider first spins to

secure himself firmly to the leaf; thus producing, as Mr. Forbes

remarks, a living bait for butterflies and other insects so artfully

contrived as to deceive a pair of human eyes, even when intently

examining it.[79]

A native species of spider (Thomisus citreus) exhibits a somewhat

similar alluring protection by its close resemblance to buds of the

wayfaring tree, Viburnum lantana. It is pure creamy-white, the abdomen

exactly resembling in shape and colour the unopened buds of the flowers

among which it takes its station; and it has been seen to capture flies

which came to the flowers.

But the most curious and beautiful case of alluring protection is that

of a wingless Mantis in India, which is so formed and coloured as to

resemble a pink orchis or some other fantastic flower. The whole insect

is of a bright pink colour, the large and oval abdomen looking like the

labellum of an orchid. On each side, the two posterior legs have

immensely dilated and flattened thighs which represent the petals of a

flower, while the neck and forelegs imitate the upper sepal and column

of an orchid. The insect rests motionless, in this symmetrical attitude,

among bright green foliage, being of course very conspicuous, but so

exactly resembling a flower that butterflies and other insects settle

upon it and are instantly captured. It is a living trap, baited in the

most alluring manner to catch the unwary flower-haunting insects.[80]

\_The Coloration of Birds' Eggs.\_

The colours of birds' eggs have long been a difficulty on the theory of

adaptive coloration, because, in so many cases it has not been easy to

see what can be the use of the particular colours, which are often so

bright and conspicuous that they seem intended to attract attention

rather than to be concealed. A more careful consideration of the subject

in all its bearings shows, however, that here too, in a great number of

cases, we have examples of protective coloration. When, therefore, we

cannot see the meaning of the colour, we may suppose that it has been

protective in some ancestral form, and, not being hurtful, has persisted

under changed conditions which rendered the protection needless.

We may divide all eggs, for our present purpose, into two great

divisions; those which are white or nearly so, and those which are

distinctly coloured or spotted. Egg-shells being composed mainly of

carbonate of lime, we may assume that the primitive colour of birds'

eggs was white, a colour that prevails now among the other egg-bearing

vertebrates--lizards, crocodiles, turtles, and snakes; and we might,

therefore, expect that this colour would continue where its presence had

no disadvantages. Now, as a matter of fact, we find that in all the

groups of birds which lay their eggs in concealed places, whether in

holes of trees or in the ground, or in domed or covered nests, the eggs

are either pure white or of very pale uniform coloration. Such is the

case with kingfishers, bee-eaters, penguins, and puffins, which nest in

holes in the ground; with the great parrot family, the woodpeckers, the

rollers, hoopoes, trogons, owls, and some others, which build in holes

in trees or other concealed places; while martins, wrens,

willow-warblers, and Australian finches, build domed or covered nests,

and usually have white eggs.

There are, however, many other birds which lay their white eggs in open

nests; and these afford some very interesting examples of the varied

modes by which concealment may be obtained. All the duck tribe, the

grebes, and the pheasants belong to this class; but these birds all have

the habit of covering their eggs with dead leaves or other material

whenever they leave the nest, so as effectually to conceal them. Other

birds, as the short-eared owl, the goatsucker, the partridge, and some

of the Australian ground pigeons, lay their white or pale eggs on the

bare soil; but in these cases the birds themselves are protectively

coloured, so that, when sitting, they are almost invisible; and they

have the habit of sitting close and almost continuously, thus

effectually concealing their eggs.

Pigeons and doves offer a very curious case of the protection of exposed

eggs. They usually build very slight and loose nests of sticks and

twigs, so open that light can be seen through them from below, while

they are generally well concealed by foliage above. Their eggs are white

and shining; yet it is a difficult matter to discover, from beneath,

whether there are eggs in the nest or not, while they are well hidden by

the thick foliage above. The Australian podargihuge goatsuckers--build

very similar nests, and their white eggs are protected in the same

manner. Some large and powerful birds, as the swans, herons, pelicans,

cormorants, and storks, lay white eggs in open nests; but they keep

careful watch over them, and are able to drive away intruders. On the

whole, then, we see that, while white eggs are conspicuous, and

therefore especially liable to attack by egg-eating animals, they are

concealed from observation in many and various ways. We may, therefore,

assume that, in cases where there seems to be no such concealment, we

are too ignorant of the whole of the conditions to form a correct

judgment.

We now come to the large class of coloured or richly spotted eggs, and

here we have a more difficult task, though many of them decidedly

exhibit protective tints or markings. There are two birds which nest on

sandy shores--the lesser tern and the ringed plover,--and both lay

sand-coloured eggs, the former spotted so as to harmonise with coarse

shingle, the latter minutely speckled like fine sand, which are the

kinds of ground the two birds choose respectively for their nests. "The

common sandpipers' eggs assimilate so closely with the tints around them

as to make their discovery a matter of no small difficulty, as every

oologist can testify who has searched for them. The pewits' eggs, dark

in ground colour and boldly marked, are in strict harmony with the sober

tints of moor and fallow, and on this circumstance alone their

concealment and safety depend. The divers' eggs furnish another example

of protective colour; they are generally laid close to the water's edge,

amongst drift and shingle, where their dark tints and black spots

conceal them by harmonising closely with surrounding objects. The snipes

and the great army of sandpipers furnish innumerable instances of

protectively coloured eggs. In all the instances given the sitting-bird

invariably leaves the eggs uncovered when it quits them, and

consequently their safety depends solely on the colours which adorn

them."[81] The wonderful range of colour and marking in the eggs of the

guillemot may be imputed to the inaccessible rocks on which it breeds,

giving it complete protection from enemies. Thus the pale or bluish

ground colour of the eggs of its allies, the auks and puffins, has

become intensified and blotched and spotted in the most marvellous

variety of patterns, owing to there being no selective agency to prevent

individual variation having full sway.

The common black coot (Fulica atra) has eggs which are coloured in a

specially protective manner. Dr. William Marshall writes, that it only

breeds in certain localities where a large water reed (Phragmites

arundinacea) abounds. The eggs of the coot are stained and spotted with

black on a yellowish-gray ground, and the dead leaves of the reed are of

the same colour, and are stained black by small parasitic fungi of the

Uredo family; and these leaves form the bed on which the eggs are laid.

The eggs and the leaves agree so closely in colour and markings that it

is a difficult thing to distinguish the eggs at any distance. It is to

be noted that the coot never covers up its eggs, as its ally the

moor-hen usually does.

The beautiful blue or greenish eggs of the hedge-sparrow, the

song-thrush, and sometimes those of the blackbird, seem at first sight

especially calculated to attract attention, but it is very doubtful

whether they are really so conspicuous when seen at a little distance

among their usual surroundings. For the nests of these birds are either

in evergreens, as holly or ivy, or surrounded by the delicate green

tints of our early spring vegetation, and may thus harmonise very well

with the colours around them. The great majority of the eggs of our

smaller birds are so spotted or streaked with brown or black on

variously tinted grounds that, when lying in the shadow of the nest and

surrounded by the many colours and tints of bark and moss, of purple

buds and tender green or yellow foliage, with all the complex glittering

lights and mottled shades produced among these by the spring sunshine

and by sparkling raindrops, they must have a quite different aspect from

that which they possess when we observe them torn from their natural

surroundings. We have here, probably, a similar case of general

protective harmony to that of the green caterpillars with beautiful

white or purple bands and spots, which, though gaudily conspicuous when

seen alone, become practically invisible among the complex lights and

shadows of the foliage they feed upon.

In the case of the cuckoo, which lays its eggs in the nests of a variety

of other birds, the eggs themselves are subject to considerable

variations of colour, the most common type, however, resembling those of

the pipits, wagtails, or warblers, in whose nests they are most

frequently laid. It also often lays in the nest of the hedge-sparrow,

whose bright blue eggs are usually not at all nearly matched, although

they are sometimes said to be so on the Continent. It is the opinion of

many ornithologists that each female cuckoo lays the same coloured eggs,

and that it usually chooses a nest the owners of which lay somewhat

similar eggs, though this is by no means universally the case. Although

birds which have cuckoos' eggs imposed upon them do not seem to neglect

them on account of any difference of colour, yet they probably do so

occasionally; and if, as seems probable, each bird's eggs are to some

extent protected by their harmony of colour with their surroundings, the

presence of a larger and very differently coloured egg in the nest might

be dangerous, and lead to the destruction of the whole set. Those

cuckoos, therefore, which most frequently placed their eggs among the

kinds which they resembled, would in the long run leave most progeny,

and thus the very frequent accord in colour might have been brought

about.

Some writers have suggested that the varied colours of birds' eggs are

primarily due to the effect of surrounding coloured objects on the

female bird during the period preceding incubation; and have expended

much ingenuity in suggesting the objects that may have caused the eggs

of one bird to be blue, another brown, and another pink.[82] But no

evidence has been presented to prove that any effects whatever are

produced by this cause, while there seems no difficulty in accounting

for the facts by individual variability and the action of natural

selection. The changes that occur in the conditions of existence of

birds must sometimes render the concealment less perfect than it may

once have been; and when any danger arises from this cause, it may be

met either by some change in the colour of the eggs, or in the

structure or position of the nest, or by the increased care which the

parents bestow upon the eggs. In this way the various divergences which

now so often puzzle us may have arisen.

\_Colour as a Means of Recognition.\_

If we consider the habits and life-histories of those animals which are

more or less gregarious, comprising a large proportion of the herbivora,

some carnivora, and a considerable number of all orders of birds, we

shall see that a means of ready recognition of its own kind, at a

distance or during rapid motion, in the dusk of twilight or in partial

cover, must be of the greatest advantage and often lead to the

preservation of life. Animals of this kind will not usually receive a

stranger into their midst. While they keep together they are generally

safe from attack, but a solitary straggler becomes an easy prey to the

enemy; it is, therefore, of the highest importance that, in such a case,

the wanderer should have every facility for discovering its companions

with certainty at any distance within the range of vision.

Some means of easy recognition must be of vital importance to the young

and inexperienced of each flock, and it also enables the sexes to

recognise their kind and thus avoid the evils of infertile crosses; and

I am inclined to believe that its necessity has had a more widespread

influence in determining the diversities of animal coloration than any

other cause whatever. To it may probably be imputed the singular fact

that, whereas bilateral symmetry of coloration is very frequently lost

among domesticated animals, it almost universally prevails in a state of

nature; for if the two sides of an animal were unlike, and the diversity

of coloration among domestic animals occurred in a wild state, easy

recognition would be impossible among numerous closely allied forms.[83]

The wonderful diversity of colour and of marking that prevails,

especially in birds and insects, may be due to the fact that one of the

first needs of a new species would be, to keep separate from its nearest

allies, and this could be most readily done by some easily seen external

mark of difference. A few illustrations will serve to show how this

principle acts in nature.

My attention was first called to the subject by a remark of Mr. Darwin's

that, though, "the hare on her form is a familiar instance of

concealment through colour, yet the principle partly fails in a closely

allied species, the rabbit; for when running to its burrow it is made

conspicuous to the sportsman, and no doubt to all beasts of prey, by its

upturned white tail."[84] But a little consideration of the habits of

the animal will show that the white upturned tail is of the greatest

value, and is really, as it has been termed by a writer in \_The Field\_,

a "signal flag of danger." For the rabbit is usually a crepuscular

animal, feeding soon after sunset or on moonlight nights. When disturbed

or alarmed it makes for its burrow, and the white upturned tails of

those in front serve as guides and signals to those more remote from

home, to the young and the feeble; and thus each following the one or

two before it, all are able with the least possible delay to regain a

place of comparative safety. The apparent danger, therefore, becomes a

most important means of security.

The same general principle enables us to understand the singular, and

often conspicuous, markings on so many gregarious herbivora which are

yet, on the whole, protectively coloured. Thus, the American prong-buck

has a white patch behind and a black muzzle. The Tartarian antelope, the

Ovis poli of High Asia, the Java wild ox, several species of deer, and a

large number of antelopes have a similar conspicuous white patch behind,

which, in contrast to the dusky body, must enable them to be seen and

followed from a distance by their fellows. Where there are many species

of nearly the same general size and form inhabiting the same region--as

with the antelopes of Africa--we find many distinctive markings of a

similar kind. The gazelles have variously striped and banded faces,

besides white patches behind and on the flanks, as shown in the woodcut.

The spring-bok has a white patch on the face and one on the sides, with

a curiously distinctive white stripe above the tail, which is nearly

concealed when the animal is at rest by a fold of skin but comes into

full view when it is in motion, being thus quite analogous to the

upturned white tail of the rabbit. In the pallah the white rump-mark is

bordered with black, and the peculiar shape of the horns distinguishes

it when seen from the front. The sable-antelope, the gems-bok, the oryx,

the hart-beest, the bonte-bok, and the addax have each peculiar white

markings; and they are besides characterised by horns so remarkably

different in each species and so conspicuous, that it seems probable

that the peculiarities in length, twist, and curvature have been

differentiated for the purpose of recognition, rather than for any

speciality of defence in species whose general habits are so similar.

[Illustration: FIG. 18.--Gazella soemmerringi.]

It is interesting to note that these markings for recognition are very

slightly developed in the antelopes of the woods and marshes. Thus, the

grys-bok is nearly uniform in colour, except the long black-tipped ears;

and it frequents the wooded mountains. The duyker-bok and the rhoode-bok

are wary bush-haunters, and have no marks but the small white patch

behind. The wood-haunting bosch-bok goes in pairs, and has hardly any

distinctive marks on its dusky chestnut coat, but the male alone is

horned. The large and handsome koodoo frequents brushwood, and its

vertical white stripes are no doubt protective, while its magnificent

spiral horns afford easy recognition. The eland, which is an inhabitant

of the open country, is uniformly coloured, being sufficiently

recognisable by its large size and distinctive form; but the Derbyan

eland is a forest animal, and has a protectively striped coat. In like

manner, the fine Speke's antelope, which lives entirely in the swamps

and among reeds, has pale vertical stripes on the sides (protective),

with white markings on face and breast for recognition. An inspection of

the figures of antelopes and other animals in Wood's \_Natural History\_,

or in other illustrated works, will give a better idea of the

peculiarities of recognition markings than any amount of description.

Other examples of such coloration are to be seen in the dusky tints of

the musk-sheep and the reindeer, to whom recognition at a distance on

the snowy plains is of more importance than concealment from their few

enemies. The conspicuous stripes and bands of the zebra and the quagga

are probably due to the same cause, as may be the singular crests and

face-marks of several of the monkeys and lemurs.[85]

[Illustration: FIG. 19--Recognition marks of three African plovers.]

Among birds, these recognition marks are especially numerous and

suggestive. Species which inhabit open districts are usually

protectively coloured; but they generally possess some distinctive

markings for the purpose of being easily recognised by their kind, both

when at rest and during flight. Such are, the white bands or patches on

the breast or belly of many birds, but more especially the head and neck

markings in the form of white or black caps, collars, eye-marks or

frontal patches, examples of which are seen in the three species of

African plovers figured on page 221.

Recognition marks during flight are very important for all birds which

congregate in flocks or which migrate together; and it is essential

that, while being as conspicuous as possible, the marks shall not

interfere with the general protective tints of the species when at rest.

Hence they usually consist of well-contrasted markings on the wings and

tail, which are concealed during repose but become fully visible when

the bird takes flight. Such markings are well seen in our four British

species of shrikes, each having quite different white marks on the

expanded wings and on the tail feathers; and the same is the case with

our three species of Saxicola--the stone-chat, whin-chat, and

wheat-ear--which are thus easily recognisable on the wing, especially

when seen from above, as they would be by stragglers looking out for

their companions. The figures opposite, of the wings of two African

species of stone-curlew which are sometimes found in the same districts,

well illustrates these specific recognition marks. Though not very

greatly different to our eyes, they are no doubt amply so to the sharp

vision of the birds themselves.

Besides the white patches on the primaries here shown, the secondary

feathers are, in some cases, so coloured as to afford very distinctive

markings during flight, as seen in the central secondary quills of two

African coursers (Fig. 21).

[Illustration: FIG. 20.--Oedicnemus vermiculatus (above). Oe.

senegalensis (below).]

Most characteristic of all, however, are the varied markings of the

outer tail-feathers, whose purpose is so well shown by their being

almost always covered during repose by the two middle feathers, which

are themselves quite unmarked and protectively tinted like the rest of

the upper surface of the body. The figures of the expanded tails of two

species of East Asiatic snipe, whose geographical ranges overlap each

other, will serve to illustrate this difference; which is frequently

much greater and modified in an endless variety of ways (Fig. 22).

Numbers of species of pigeons, hawks, finches, warblers, ducks, and

innumerable other birds possess this class of markings; and they

correspond so exactly in general character with those of the mammalia,

already described, that we cannot doubt they serve a similar

purpose.[86]

[Illustration: FIG. 21.--Secondary quills.]

[Illustration: FIG. 22.--Scolopax megala (upper). S. stenura (lower).]

Those birds which are inhabitants of tropical forests, and which need

recognition marks that shall be at all times visible among the dense

foliage, and not solely or chiefly during flight, have usually small but

brilliant patches of colour on the head or neck, often not interfering

with the generally protective character of their plumage. Such are the

bright patches of blue, red, or yellow, by which the usually green

Eastern barbets are distinguished; and similar bright patches of colour

characterise the separate species of small green fruit-doves. To this

necessity for specialisation in colour, by which each bird may easily

recognise its kind, is probably due that marvellous variety in the

peculiar beauties of some groups of birds. The Duke of Argyll, speaking

of the humming birds, made the objection that "A crest of topaz is no

better in the struggle for existence than a crest of sapphire. A frill

ending in spangles of the emerald is no better in the battle of life

than a frill ending in spangles of the ruby. A tail is not affected for

the purposes of flight, whether its marginal or its central feathers are

decorated with white;" and he goes on to urge that mere beauty and

variety for their own sake are the only causes of these differences.

But, on the principles here suggested, the divergence itself is useful,

and must have been produced \_pari passu\_ with the structural differences

on which the differentiation of species depends; and thus we have

explained the curious fact that prominent differences of colour often

distinguish species otherwise very closely allied to each other.

Among insects, the principle of distinctive coloration for recognition

has probably been at work in the production of the wonderful diversity

of colour and marking we find everywhere, more especially among the

butterflies and moths; and here its chief function may have been to

secure the pairing together of individuals of the same species. In some

of the moths this has been secured by a peculiar odour, which attracts

the males to the females from a distance; but there is no evidence that

this is universal or even general, and among butterflies, especially,

the characteristic colour and marking, aided by size and form, afford

the most probable means of recognition. That this is so is shown by the

fact that "the common white butterfly often flies down to a bit of paper

on the ground, no doubt mistaking it for one of its own species;" while,

according to Mr. Collingwood, in the Malay Archipelago, "a dead

butterfly pinned upon a conspicuous twig will often arrest an insect of

the same species in its headlong flight, and bring it down within easy

reach of the net, especially if it be of the opposite sex."[87] In a

great number of insects, no doubt, form, motions, stridulating sounds,

or peculiar odours, serve to distinguish allied species from each other,

and this must be especially the case with nocturnal insects, or with

those whose colours are nearly uniform and are determined by the need of

protection; but by far the larger number of day-flying and active

insects exhibit varieties of colour and marking, forming the most

obvious distinction between allied species, and which have, therefore,

in all probability been acquired in the process of differentiation for

the purpose of checking the intercrossing of closely allied forms.[88]

Whether this principle extends to any of the less highly organised

animals is doubtful, though it may perhaps have affected the higher

mollusca. But in marine animals it seems probable that the colours,

however beautiful, varied, and brilliant they may often be, are in most

cases protective, assimilating them to the various bright-coloured

seaweeds, or to some other animals which it is advantageous for them to

imitate.[89]

\_Summary of the Preceding Exposition.\_

Before proceeding to discuss some of the more recondite phenomena of

animal coloration, it will be well to consider for a moment the extent

of the ground we have already covered. Protective coloration, in some of

its varied forms, has not improbably modified the appearance of one-half

of the animals living on the globe. The white of arctic animals, the

yellowish tints of the desert forms, the dusky hues of crepuscular and

nocturnal species, the transparent or bluish tints of oceanic creatures,

represent a vast host in themselves; but we have an equally numerous

body whose tints are adapted to tropical foliage, to the bark of trees,

or to the soil or dead leaves on or among which they habitually live.

Then we have the innumerable special adaptations to the tints and forms

of leaves, or twigs, or flowers; to bark or moss; to rock or pebble; by

which such vast numbers of the insect tribes obtain protection; and we

have seen that these various forms of coloration are equally prevalent

in the waters of the seas and oceans, and are thus coextensive with the

domain of life upon the earth. The comparatively small numbers which

possess "terrifying" or "alluring" coloration may be classed under the

general head of the protectively coloured.

But under the next head--colour for recognition--we have a totally

distinct category, to some extent antagonistic or complementary to the

last, since its essential principle is visibility rather than

concealment. Yet it has been shown, I think, that this mode of

coloration is almost equally important, since it not only aids in the

preservation of existing species and in the perpetuation of pure races,

but was, perhaps, in its earlier stages, a not unimportant factor in

their development. To it we owe most of the variety and much of the

beauty in the colours of animals; it has caused at once bilateral

symmetry and general permanence of type; and its range of action has

been perhaps equally extensive with that of coloration for concealment.

\_Influence of Locality or of Climate on Colour.\_

Certain relations between locality and coloration have long been

noticed. Mr. Gould observed that birds from inland or continental

localities were more brightly coloured than those living near the

sea-coast or on islands, and he supposed that the more brilliant

atmosphere of the inland stations was the explanation of the

phenomenon.[90] Many American naturalists have observed similar facts,

and they assert that the intensity of the colours of birds and mammals

increases from north to south, and also with the increase of humidity.

This change is imputed by Mr. J.A. Allen to the direct action of the

environment. He says: "In respect to the correlation of intensity of

colour in animals with the degree of humidity, it would perhaps be more

in accordance with cause and effect to express the law of correlation as

a \_decrease\_ of intensity of colour with a \_decrease\_ of humidity, the

paleness evidently resulting from exposure and the blanching effect of

intense sunlight, and a dry, often intensely heated atmosphere. With the

decrease of the aqueous precipitation the forest growth and the

protection afforded by arborescent vegetation gradually also decreases,

as of course does also the protection afforded by clouds, the

excessively humid regions being also regions of extreme cloudiness,

while the dry regions are comparatively cloudless districts."[91] Almost

identical changes occur in birds, and are imputed by Mr. Allen to

similar causes.

It will be seen that Mr. Gould and Mr. Allen impute opposite effects to

the same cause, brilliancy or intensity of colour being due to a

brilliant atmosphere according to the former, while paleness of colour

is imputed by the latter to a too brilliant sun. According to the

principles which have been established by the consideration of arctic,

desert, and forest animals respectively, we shall be led to conclude

that there has been no direct action in this case, but that the effects

observed are due to the greater or less need of protection. The pale

colour that is prevalent in arid districts is in harmony with the

general tints of the surface; while the brighter tints or more intense

coloration, both southward and in humid districts, are sufficiently

explained by the greater shelter due to a more luxuriant vegetation and

a shorter winter. The advocates of the theory that intensity of light

directly affects the colours of organisms, are led into perpetual

inconsistencies. At one time the brilliant colours of tropical birds and

insects are imputed to the intensity of a tropical sun, while the same

intensity of sunlight is now said to have a "bleaching" effect. The

comparatively dull and sober hues of our northern fauna were once

supposed to be the result of our cloudy skies; but now we are told that

cloudy skies and a humid atmosphere intensify colour.

In my \_Tropical Nature\_ (pp. 257-264) I have called attention to what is

perhaps the most curious and decided relation of colour to locality

which has yet been observed--the prevalence of white markings in the

butterflies and birds of islands.

So many cases are adduced from so many different islands, both in the

eastern and western hemisphere, that it is impossible to doubt the

existence of some common cause; and it seems probable to me now, after a

fuller consideration of the whole subject of colour, that here too we

have one of the almost innumerable results of the principle of

protective coloration. White is, as a rule, an uncommon colour in

animals, but probably only because it is so conspicuous. Whenever it

becomes protective, as in the case of arctic animals and aquatic birds,

it appears freely enough; while we know that white varieties of many

species occur occasionally in the wild state, and that, under

domestication, white or parti-coloured breeds are freely produced. Now

in all the islands in which exceptionally white-marked birds and

butterflies have been observed, we find two features which would tend to

render the conspicuous white markings less injurious--a luxuriant

tropical vegetation, and a decided scarcity of rapacious mammals and

birds. White colours, therefore, would not be eliminated by natural

selection; but variations in this direction would bear their part in

producing the recognition marks which are everywhere essential, and

which, in these islands, need not be so small or so inconspicuous as

elsewhere.

\_Concluding Remarks.\_

On a review of the whole subject, then, we must conclude that there is

no evidence of the individual or prevalent colours of organisms being

directly determined by the amount of light, or heat, or moisture, to

which they are exposed; while, on the other hand, the two great

principles of the need of concealment from enemies or from their prey,

and of recognition by their own kind, are so wide-reaching in their

application that they appear at first sight to cover almost the whole

ground of animal coloration. But, although they are indeed wonderfully

general and have as yet been very imperfectly studied, we are acquainted

with other modes of coloration which have a different origin. These

chiefly appertain to the very singular class of warning colours, from

which arise the yet more extraordinary phenomena of mimicry; and they

open up so curious a field of inquiry and present so many interesting

problems, that a chapter must be devoted to them. Yet another chapter

will be required by the subject of sexual differentiation of colour and

ornament, as to the origin and meaning of which I have arrived at

different conclusions from Mr. Darwin. These various forms of coloration

having been discussed and illustrated, we shall be in a position to

attempt a brief sketch of the fundamental laws which have determined the

general coloration of the animal world.

FOOTNOTES:

[Footnote 65: \_Proceedings of the Royal Society\_, No. 243, 1886;

\_Transactions of the Royal Society\_, vol. clxxviii. B. pp. 311-441.]

[Footnote 66: \_A Naturalist's Wanderings in the Eastern Archipelago\_, p.

460.]

[Footnote 67: \_Trans. Phil. Soc.\_ (? \_of S. Africa\_), 1878, part iv, p.

27.]

[Footnote 68: \_Proc. Zool. Soc.\_, 1862 p. 357.]

[Footnote 69: With reference to this general resemblance of insects to

their environment the following remarks by Mr. Poulton are very

instructive. He says: "Holding the larva of Sphinx ligustri in one hand

and a twig of its food-plant in the other, the wonder we feel is, not at

the resemblance but at the difference; we are surprised at the

difficulty experienced in detecting so conspicuous an object. And yet

the protection is very real, for the larvae will be passed over by those

who are not accustomed to their appearance, although the searcher may be

told of the presence of a large caterpillar. An experienced entomologist

may also fail to find the larvae till after a considerable search. This

is general protective resemblance, and it depends upon a general harmony

between the appearance of the organism and its whole environment. It is

impossible to understand the force of this protection for any larva,

without seeing it on its food-plant and in an entirely normal condition.

The artistic effect of green foliage is more complex than we often

imagine; numberless modifications are wrought by varied lights and

shadows upon colours which are in themselves far from uniform. In the

larva of Papilio machaon the protection is very real when the larva is

on the food-plant, and can hardly be appreciated at all when the two are

apart." Numerous other examples are given in the chapter on "Mimicry and

other Protective Resemblances among Animals," in my \_Contributions to

the Theory of Natural Selection\_.]

[Footnote 70: \_The Naturalist in Nicaragua\_, p. 19.]

[Footnote 71: R. Meldola, in \_Proc. Zool. Soc.\_, 1873, p. 155.]

[Footnote 72: \_Nature\_, vol. iii. p. 166.]

[Footnote 73: \_Trans. Ent. Soc. Lond.\_, 1878, p. 185.]

[Footnote 74: \_Ibid.\_ (\_Proceedings\_, p. xlii.)]

[Footnote 75: Wallace's \_Malay Archipelago\_, vol. i. p. 204 (fifth

edition, p. 130), with figure.]

[Footnote 76: Moseley's \_Notes by a Naturalist on the Challenger\_.]

[Footnote 77: \_Proceedings of the Boston Soc. of Nat. Hist.\_, vol. xiv.

1871.]

[Footnote 78: \_Nature\_, 1870, p. 376.]

[Footnote 79: \_A Naturalist's Wanderings in the Eastern Archipelago\_, p.

63.]

[Footnote 80: A beautiful drawing of this rare insect, Hymenopus

bicornis (in the nymph or active pupa state), was kindly sent me by Mr.

Wood-Mason, Curator of the Indian Museum at Calcutta. A species, very

similar to it, inhabits Java, where it is said to resemble a pink

orchid. Other Mantidae, of the genus Gongylus, have the anterior part of

the thorax dilated and coloured either white, pink, or purple; and they

so closely resemble flowers that, according to Mr. Wood-Mason, one of

them, having a bright violet-blue prothoracic shield, was found in Pegu

by a botanist, and was for a moment mistaken by him for a flower. See

\_Proc. Ent. Soc. Lond.\_, 1878, p. liii.]

[Footnote 81: C. Dixon, in Seebohm's \_History of British Birds\_, vol.

ii. Introduction, p. xxvi. Many of the other examples here cited are

taken from the same valuable work.]

[Footnote 82: See A.H.S. Lucas, in \_Proceedings of Royal Society of

Victoria\_, 1887, p. 56.]

[Footnote 83: Professor Wm.H. Brewer of Yale College has shown that the

white marks or the spots of domesticated animals are rarely symmetrical,

but have a tendency to appear more frequently on the left side. This is

the case with horses, cattle, dogs, and swine. Among wild animals the

skunk varies considerably in the amount of white on the body, and this

too was found to be usually greatest on the left side. A close

examination of numerous striped or spotted species, as tigers, leopards,

jaguars, zebras, etc., showed that the bilateral symmetry was not exact,

although the general effect of the two sides was the same. This is

precisely what we should expect if the symmetry is not the result of a

general law of the organisation, but has been, in part at least,

produced and preserved for the useful purpose of recognition by the

animal's fellows of the same species, and especially by the sexes and

the young. See \_Proc. of the Am. Ass. for Advancement of Science\_, vol.

xxx. p. 246.]

[Footnote 84: \_Descent of Man\_, p. 542.]

[Footnote 85: It may be thought that such extremely conspicuous markings

as those of the zebra would be a great danger in a country abounding

with lions, leopards, and other beasts of prey; but it is not so. Zebras

usually go in bands, and are so swift and wary that they are in little

danger during the day. It is in the evening, or on moonlight nights,

when they go to drink, that they are chiefly exposed to attack; and Mr.

Francis Galton, who has studied these animals in their native haunts,

assures me, that in twilight they are not at all conspicuous, the

stripes of white and black so merging together into a gray tint that it

is very difficult to see them at a little distance. We have here an

admirable illustration of how a glaringly conspicuous style of marking

for recognition may be so arranged as to become also protective at the

time when protection is most needed; and we may also learn how

impossible it is for us to decide on the inutility of any kind of

coloration without a careful study of the habits of the species in its

native country.]

[Footnote 86: The principle of colouring for recognition was, I believe,

first stated in my article on "The Colours of Animals and Plants" in

Macmillan's \_Magazine\_, and more fully in my volume on \_Tropical

Nature\_. Subsequently Mrs. Barber gave a few examples under the head of

"Indicative or Banner Colours," but she applied it to the distinctive

colours of the males of birds, which I explain on another principle,

though this may assist.]

[Footnote 87: Quoted by Darwin in \_Descent of Man\_, p. 317.]

[Footnote 88: In the \_American Naturalist\_ of March 1888, Mr. J.E. Todd

has an article on "Directive Coloration in Animals," in which he

recognises many of the cases here referred to, and suggests a few

others, though I think he includes many forms of coloration--as

"paleness of belly and inner side of legs"--which do not belong to this

class.]

[Footnote 89: For numerous examples of this protective colouring of

marine animals see Moseley's \_Voyage of the Challenger\_, and Dr. E.S.

Morse in \_Proc. of Bost. Soc. of Nat. Hist.\_, vol. xiv. 1871.]

[Footnote 90: See \_Origin of Species\_, p. 107.]

[Footnote 91: The "Geographical Variation of North American Squirrels,"

\_Proc. Bost. Soc. of Nat. Hist.\_, 1874, p. 284; and \_Mammals and Winter

Birds of Florida\_, pp. 233-241.]

CHAPTER IX

WARNING COLORATION AND MIMICRY

The skunk as an example of warning coloration--Warning colours

among insects--Butterflies--Caterpillars--Mimicry--How mimicry

has been produced--Heliconidae--Perfection of the

imitation--Other cases of mimicry among Lepidoptera--Mimicry

among protected groups--Its explanation--Extension of the

principle--Mimicry in other orders of insects--Mimicry among the

vertebrata--Snakes--The rattlesnake and the cobra--Mimicry among

birds--Objections to the theory of mimicry--Concluding remarks

on warning colours and mimicry.

We have now to deal with a class of colours which are the very opposite

of those we have hitherto considered, since, instead of serving to

conceal the animals that possess them or as recognition marks to their

associates, they are developed for the express purpose of rendering the

species conspicuous. The reason of this is that the animals in question

are either the possessors of some deadly weapons, as stings or poison

fangs, or they are uneatable, and are thus so disagreeable to the usual

enemies of their kind that they are never attacked when their peculiar

powers or properties are known. It is, therefore, important that they

should not be mistaken for defenceless or eatable species of the same

class or order, since in that case they might suffer injury, or even

death, before their enemies discovered the danger or the uselessness of

the attack. They require some signal or danger-flag which shall serve as

a warning to would-be enemies not to attack them, and they have usually

obtained this in the form of conspicuous or brilliant coloration, very

distinct from the protective tints of the defenceless animals allied to

them.

\_The Skunk as illustrating Warning Coloration.\_

While staying a few days, in July 1887, at the Summit Hotel on the

Central Pacific Railway, I strolled out one evening after dinner, and on

the road, not fifty yards from the house, I saw a pretty little white

and black animal with a bushy tail coming towards me. As it came on at a

slow pace and without any fear, although it evidently saw me, I thought

at first that it must be some tame creature, when it suddenly occurred

to me that it was a skunk. It came on till within five or six yards of

me, then quietly climbed over a dwarf wall and disappeared under a small

outhouse, in search of chickens, as the landlord afterwards told me.

This animal possesses, as is well known, a most offensive secretion,

which it has the power of ejecting over its enemies, and which

effectually protects it from attack. The odour of this substance is so

penetrating that it taints, and renders useless, everything it touches,

or in its vicinity. Provisions near it become uneatable, and clothes

saturated with it will retain the smell for several weeks, even though

they are repeatedly washed and dried. A drop of the liquid in the eyes

will cause blindness, and Indians are said not unfrequently to lose

their sight from this cause. Owing to this remarkable power of offence

the skunk is rarely attacked by other animals, and its black and white

fur, and the bushy white tail carried erect when disturbed, form the

danger-signals by which it is easily distinguished in the twilight or

moonlight from unprotected animals. Its consciousness that it needs only

to be seen to be avoided gives it that slowness of motion and

fearlessness of aspect which are, as we shall see, characteristic of

most creatures so protected.

\_Warning Colours among Insects.\_

It is among insects that warning colours are best developed, and most

abundant. We all know how well marked and conspicuous are the colours

and forms of the stinging wasps and bees, no one of which in any part of

the world is known to be protectively coloured like the majority of

defenceless insects. Most of the great tribe of Malacoderms among

beetles are distasteful to insect-eating animals. Our red and black

Telephoridae, commonly called "soldiers and sailors," were found, by Mr.

Jenner Weir, to be refused by small birds. These and the allied

Lampyridae (the fireflies and glow-worms) in Nicaragua, were rejected by

Mr. Belt's tame monkey and by his fowls, though most other insects were

greedily eaten by them. The Coccinellidae or lady-birds are another

uneatable group, and their conspicuous and singularly spotted bodies

serve to distinguish them at a glance from all other beetles.

These uneatable insects are probably more numerous than is supposed,

although we already know immense numbers that are so protected. The most

remarkable are the three families of butterflies--Heliconidae, Danaidae,

and Acraeidae--comprising more than a thousand species, and

characteristic respectively of the three great tropical regions--South

America, Southern Asia, and Africa. All these butterflies have

peculiarities which serve to distinguish them from every other group in

their respective regions. They all have ample but rather weak wings, and

fly slowly; they are always very abundant; and they all have conspicuous

colours or markings, so distinct from those of other families that, in

conjunction with their peculiar outline and mode of flight, they can

usually be recognised at a glance. Other distinctive features are, that

their colours are always nearly the same on the under surface of their

wings as on the upper; they never try to conceal themselves, but rest on

the upper surfaces of leaves or flowers; and, lastly, they all have

juices which exhale a powerful scent, so that when one kills them by

pinching the body, the liquid that exudes stains the fingers yellow, and

leaves an odour that can only be removed by repeated washings.

Now, there is much direct evidence to show that this odour, though not

very offensive to us, is so to most insect-eating creatures. Mr. Bates

observed that, when set out to dry, specimens of Heliconidae were less

subject to the attacks of vermin; while both he and I noticed that they

were not attacked by insect-eating birds or dragonflies, and that their

wings were not found in the forest paths among the numerous wings of

other butterflies whose bodies had been devoured. Mr. Belt once observed

a pair of birds capturing insects for their young; and although the

Heliconidae swarmed in the vicinity, and from their slow flight could

have been easily caught, not one was ever pursued, although other

butterflies did not escape. His tame monkey also, which would greedily

munch up other butterflies, would never eat the Heliconidae. It would

sometimes smell them, but always rolled them up in its hand and then

dropped them.

We have also some corresponding evidence as to the distastefulness of

the Eastern Danaidae. The Hon. Mr. Justice Newton, who assiduously

collected and took notes upon the Lepidoptera of Bombay, informed Mr.

Butler of the British Museum that the large and swift-flying butterfly

Charaxes psaphon, was continually persecuted by the bulbul, so that he

rarely caught a specimen of this species which had not a piece snipped

out of the hind wings. He offered one to a bulbul which he had in a

cage, and it was greedily devoured, whilst it was only by repeated

persecution that he succeeded in inducing the bird to touch a

Danais.[92]

Besides these three families of butterflies, there are certain groups of

the great genus Papilio--the true swallow-tailed butterflies--which have

all the characteristics of uneatable insects. They have a special

coloration, usually red and black (at least in the females), they fly

slowly, they are very abundant, and they possess a peculiar odour

somewhat like that of the Heliconidae. One of these groups is common in

tropical America, another in tropical Asia, and it is curious that,

although not very closely allied, they have each the same red and black

colours, and are very distinct from all the other butterflies of their

respective countries. There is reason to believe also that many of the

brilliantly coloured and weak-flying diurnal moths, like the fine

tropical Agaristidae and burnet-moths, are similarly protected, and that

their conspicuous colours serve as a warning of inedibility. The common

burnet-moth (Anthrocera filipendula) and the equally conspicuous

ragwort-moth (Euchelia jacobeae) have been proved to be distasteful to

insect-eating creatures.

The most interesting and most conclusive example of warning coloration

is, however, furnished by caterpillars, because in this case the facts

have been carefully ascertained experimentally by competent observers.

In the year 1866, when Mr. Darwin was collecting evidence as to the

supposed effect of sexual selection in bringing about the brilliant

coloration of the higher animals, he was struck by the fact that many

caterpillars have brilliant and conspicuous colours, in the production

of which sexual selection could have no place. We have numbers of such

caterpillars in this country, and they are characterised not only by

their gay colours but by not concealing themselves. Such are the mullein

and the gooseberry caterpillars, the larvae of the spurge hawk-moth, of

the buff-tip, and many others. Some of these caterpillars are

wonderfully conspicuous, as in the case of that noticed by Mr. Bates in

South America, which was four inches long, banded across with black and

yellow, and with bright red head, legs, and tail. Hence it caught the

eye of any one who passed by, even at the distance of many yards.

Mr. Darwin asked me to try and suggest some explanation of this

coloration; and, having been recently interested in the question of the

warning coloration of butterflies, I suggested that this was probably a

similar case,--that these conspicuous caterpillars were distasteful to

birds and other insect-eating creatures, and that their bright

non-protective colours and habit of exposing themselves to view, enabled

their enemies to distinguish them at a glance from the edible kinds and

thus learn not to touch them; for it must be remembered that the bodies

of caterpillars while growing are so delicate, that a wound from a

bird's beak would be perhaps as fatal as if they were devoured.[93] At

this time not a single experiment or observation had been made on the

subject, but after I had brought the matter before the Entomological

Society, two gentlemen, who kept birds and other tame animals, undertook

to make experiments with a variety of caterpillars.

Mr. Jenner Weir was the first to experiment with ten species of small

birds in his aviary, and he found that none of them would eat the

following smooth-skinned conspicuous caterpillars--Abraxas

grossulariata, Diloba caeruleocephala, Anthrocera filipendula, and

Cucullia verbasci. He also found that they would not touch any hairy or

spiny larvae, and he was satisfied that it was not the hairs or the

spines, but the unpleasant taste that caused them to be rejected,

because in one case a young smooth larva of a hairy species, and in

another case the pupa of a spiny larva, were equally rejected. On the

other hand, all green or brown caterpillars as well as those that

resemble twigs were greedily devoured.[94]

Mr. A.G. Butler also made experiments with some green lizards (Lacerta

viridis), which greedily ate all kinds of food, including flies of many

kinds, spiders, bees, butterflies, and green caterpillars; but they

would not touch the caterpillar of the gooseberry-moth (Abraxas

grossulariata), or the imago of the burnet-moth (Anthrocera

filipendula). The same thing happened with frogs. When the gooseberry

caterpillars were first given to them, "they sprang forward and licked

them eagerly into their mouths; no sooner, however, had they done so,

than they seemed to become aware of the mistake that they had made, and

sat with gaping mouths, rolling their tongues about, until they had got

quit of the nauseous morsels, which seemed perfectly uninjured, and

walked off as briskly as ever." Spiders seemed equally to dislike them.

This and another conspicuous caterpillar (Halia wavaria) were rejected

by two species--the geometrical garden spider (Epeira diadema) and a

hunting spider.[95]

Some further experiments with lizards were made by Professor Weismann,

quite confirming the previous observations; and in 1886 Mr. E.B. Poulton

of Oxford undertook a considerable series of experiments, with many

other species of larvae and fresh kinds of lizards and frogs. Mr.

Poulton then reviewed the whole subject, incorporating all recorded

facts, as well as some additional observations made by Mr. Jenner Weir

in 1886. More than a hundred species of larvae or of perfect insects of

various orders have now been made the subject of experiment, and the

results completely confirm my original suggestion. In almost every case

the protectively coloured larvae have been greedily eaten by all kinds

of insectivorous animals, while, in the immense majority of cases, the

conspicuous, hairy, or brightly coloured larvae have been rejected by

some or all of them. In some instances the inedibility of the larvae

extends to the perfect insect, but not in others. In the former cases

the perfect insect is usually adorned with conspicuous colours, as the

burnet and ragwort moths; but in the case of the buff-tip, the moth

resembles a broken piece of rotten stick, yet it is partly inedible,

being refused by lizards. It is, however, very doubtful whether these

are its chief enemies, and its protective form and colour may be needed

against insectivorous birds or mammals.

Mr. Samuel H. Scudder, who has largely bred North American butterflies,

has found so many of the eggs and larvae destroyed by hymenopterous and

dipterous parasites that he thinks at least nine-tenths, perhaps a

greater proportion, never reach maturity. Yet he has never found any

evidence that such parasites attack either the egg or the larva of the

inedible Danais archippus, so that in this case the insect is

distasteful to its most dangerous foes in all the stages of its

existence, a fact which serves to explain its great abundance and its

extension over almost the whole world.[96]

One case has been found of a protectively coloured larva,--one,

moreover, which in all its habits shows that it trusts to concealment to

escape its enemies--which was yet always rejected by lizards after they

had seized it, evidently under the impression that from its colour it

would be eatable. This is the caterpillar of the very common moth Mania

typica; and Mr. Poulton thinks that, in this case, the unpleasant taste

is an incidental result of some physiological processes in the organism,

and is itself a merely useless character. It is evident that the insect

would not conceal itself so carefully as it does if it had not some

enemies, and these are probably birds or small mammals, as its

food-plants are said to be dock and willow-herb, not suggestive of

places frequented by lizards; and it has been found by experiment that

lizards and birds have not always the same likes and dislikes. The case

is interesting, because it shows that nauseous fluids sometimes occur

sporadically, and may thus be intensified by natural selection when

required for the purpose of protection. Another exceptional case is

that of the very conspicuous caterpillar of the spurge hawk-moth

(Deilephila euphorbiae), which was at once eaten by a lizard, although,

as it exposes itself on its food-plant in the daytime and is very

abundant in some localities, it must almost certainly be disliked by

birds or by some animals who would otherwise devour it. If disturbed

while feeding it is said to turn round with fury and eject a quantity of

green liquid, of an acid and disagreeable smell similar to that of the

spurge milk, only worse.[97]

These facts, and Mr. Poulton's evidence that some larvae rejected by

lizards at first will be eaten if the lizards are very hungry, show that

there are differences in the amount of the distastefulness, and render

it probable that if other food were wanting many of these conspicuous

insects would be eaten. It is the abundance of the eatable kinds that

gives value to the inedibility of the smaller number; and this is

probably the reason why so many insects rely on protective colouring

rather than on the acquisition of any kind of defensive weapons. In the

long run the powers of attack and defence must balance each other. Hence

we see that even the powerful stings of bees and wasps only protect them

against some enemies, since a tribe of birds, the bee-eaters, have been

developed which feed upon them, and some frogs and lizards do so

occasionally.

The preceding outline will sufficiently explain the characteristics of

"warning coloration" and the end it serves in nature. There are many

other curious modifications of it, but these will be best appreciated

after we have discussed the remarkable phenomenon of "mimicry," which is

bound up with and altogether depends upon "warning colour," and is in

some cases the chief indication we have of the possession of some

offensive weapon to secure the safety of the species imitated.

\_Mimicry.\_

This term has been given to a form of protective resemblance, in which

one species so closely resembles another in external form and colouring

as to be mistaken for it, although the two may not be really allied and

often belong to distinct families or orders. One creature seems

disguised in order to be made like another; hence the terms "mimic" and

mimicry, which imply no voluntary action on the part of the imitator. It

has long been known that such resemblances do occur, as, for example,

the clear-winged moths of the families Sesiidae and Aegeriidae, many of

which resemble bees, wasps, ichneumons, or saw-flies, and have received

names expressive of the resemblance; and the parasitic flies (Volucella)

which closely resemble bees, on whose larvae the larvae of the flies

feed.

The great bulk of such cases remained, however, unnoticed, and the

subject was looked upon as one of the inexplicable curiosities of

nature, till Mr. Bates studied the phenomenon among the butterflies of

the Amazon, and, on his return home, gave the first rational explanation

of it.[98] The facts are, briefly, these. Everywhere in that fertile

region for the entomologist the brilliantly coloured Heliconidae abound,

with all the characteristics which I have already referred to when

describing them as illustrative of "warning coloration." But along with

them other butterflies were occasionally captured, which, though often

mistaken for them, on account of their close resemblance in form,

colour, and mode of flight, were found on examination to belong to a

very distinct family, the Pieridae. Mr. Bates notices fifteen distinct

species of Pieridae, belonging to the genera Leptalis and Euterpe, each

of which closely imitates some one species of Heliconidae, inhabiting

the same region and frequenting the same localities. It must be

remembered that the two families are altogether distinct in structure.

The larvae of the Heliconidae are tubercled or spined, the pupae

suspended head downwards, and the imago has imperfect forelegs in the

male; while the larvae of the Pieridae are smooth, the pupae are

suspended with a brace to keep the head erect, and the forefeet are

fully developed in both sexes. These differences are as large and as

important as those between pigs and sheep, or between swallows and

sparrows; while English entomologists will best understand the case by

supposing that a species of Pieris in this country was coloured and

shaped like a small tortoise-shell, while another species on the

Continent was equally like a Camberwell beauty--so like in both cases

as to be mistaken when on the wing, and the difference only to be

detected by close examination. As an example of the resemblance,

woodcuts are given of one pair in which the colours are simple, being

olive, yellow, and black, while the very distinct neuration of the wings

and form of the head and body can be easily seen.

[Illustration: FIG. 23.--Methona psidii (Heliconidae). Leptalis orise

(Pieridae).]

Besides these Pieridae, Mr. Bates found four true Papilios, seven

Erycinidae, three Castnias (a genus of day-flying moths), and fourteen

species of diurnal Bombycidae, all imitating some species of Heliconidae

which inhabited the same district; and it is to be especially noted that

none of these insects were so abundant as the Heliconidae they

resembled, generally they were far less common, so that Mr. Bates

estimated the proportion in some cases as not one to a thousand. Before

giving an account of the numerous remarkable cases of mimicry in other

parts of the world, and between various groups of insects and of higher

animals, it will be well to explain briefly the use and purport of the

phenomenon, and also the mode by which it has been brought about.

\_How Mimicry has been Produced.\_

The fact has been now established that the Heliconidae possess an

offensive odour and taste, which lead to their being almost entirely

free from attack by insectivorous creatures; they possess a peculiar

form and mode of flight, and do not seek concealment; while their

colours--although very varied, ranging from deep blue-black, with white,

yellow, or vivid red bands and spots, to the most delicate

semitransparent wings adorned with pale brown or yellow markings--are

yet always very distinctive, and unlike those of all the other families

of butterflies in the same country. It is, therefore, clear that if any

other butterflies in the same region, which are eatable and suffer great

persecution from insectivorous animals, should come to resemble any of

these uneatable species so closely as to be mistaken for them by their

enemies, they will obtain thereby immunity from persecution. This is the

obvious and sufficient reason why the imitation is useful, and therefore

why it occurs in nature. We have now to explain how it has probably been

brought about, and also why a still larger number of persecuted groups

have not availed themselves of this simple means of protection.

From the great abundance of the Heliconidae[99] all over tropical

America, the vast number of their genera and species, and their marked

distinctions from all other butterflies, it follows that they constitute

a group of high antiquity, which in the course of ages has become more

and more specialised, and owing to its peculiar advantages has now

become a dominant and aggressive race. But when they first arose from

some ancestral species or group which, owing to the food of the larvae

or some other cause, possessed disagreeable juices that caused them to

be disliked by the usual enemies of their kind, they were in all

probability not very different either in form or coloration from many

other butterflies. They would at that time be subject to repeated

attacks by insect-eaters, and, even if finally rejected, would often

receive a fatal injury. Hence arose the necessity for some

distinguishing mark, by which the devourers of butterflies in general

might learn that these particular butterflies were uneatable; and every

variation leading to such distinction, whether by form, colour, or mode

of flight, was preserved and accumulated by natural selection, till the

ancestral Heliconoids became well distinguished from eatable

butterflies, and thenceforth comparatively free from persecution. Then

they had a good time of it. They acquired lazy habits, and flew about

slowly. They increased abundantly and spread all over the country, their

larvae feeding on many plants and acquiring different habits; while the

butterflies themselves varied greatly, and colour being useful rather

than injurious to them, gradually diverged into the many coloured and

beautifully varied forms we now behold.

But, during the early stages of this process, some of the Pieridae,

inhabiting the same district, happened to be sufficiently like some of

the Heliconidae to be occasionally mistaken for them. These, of course,

survived while their companions were devoured. Those among their

descendants that were still more like Heliconidae again survived, and at

length the imitation would become tolerably perfect. Thereafter, as the

protected group diverged into distinct species of many different

colours, the imitative group would occasionally be able to follow it

with similar variations,--a process that is going on now, for Mr. Bates

informs us that in each fresh district he visited he found closely

allied representative species or varieties of Heliconidae, and along

with them species of Leptalis (Pieridae), which had varied in the same

way so as still to be exact imitations. But this process of imitation

would be subject to check by the increasing acuteness of birds and other

animals which, whenever the eatable Leptalis became numerous, would

surely find them out, and would then probably attack both these and

their friends the Heliconidae in order to devour the former and reject

the latter. The Pieridae would, however, usually be less numerous,

because their larvae are often protectively coloured and therefore

edible, while the larvae of the Heliconidae are adorned with warning

colours, spines, or tubercles, and are uneatable. It seems probable that

the larvae and pupae of the Heliconidae were the first to acquire the

protective distastefulness, both because in this stage they are more

defenceless and more liable to fatal injury, and also because we now

find many instances in which the larvae are distasteful while the

perfect insects are eatable, but I believe none in which the reverse is

the case. The larvae of the Pieridae are now beginning to acquire

offensive juices, but have not yet obtained the corresponding

conspicuous colours; while the perfect insects remain eatable, except

perhaps in some Eastern groups, the under sides of whose wings are

brilliantly coloured although this is the part which is exposed when at

rest.

It is clear that if a large majority of the larvae of Lepidoptera, as

well as the perfect insects, acquired these distasteful properties, so

as seriously to diminish the food supply of insectivorous and nestling

birds, these latter would be forced by necessity to acquire

corresponding tastes, and to eat with pleasure what some of them now eat

only under pressure of hunger; and variation and natural selection would

soon bring about this change.

Many writers have denied the possibility of such wonderful resemblances

being produced by the accumulation of fortuitous variations, but if the

reader will call to mind the large amount of variability that has been

shown to exist in all organisms, the exceptional power of rapid increase

possessed by insects, and the tremendous struggle for existence always

going on, the difficulty will vanish, especially when we remember that

nature has the same fundamental groundwork to act upon in the two

groups, general similarity of forms, wings of similar texture and

outline, and probably some original similarity of colour and marking.

Yet there is evidently considerable difficulty in the process, or with

these great resources at her command nature would have produced more of

these mimicking forms than she has done. One reason of this deficiency

probably is, that the imitators, being always fewer in number, have not

been able to keep pace with the variations of the much more numerous

imitated form; another reason may be the ever-increasing acuteness of

the enemies, which have again and again detected the imposture and

exterminated the feeble race before it has had time to become further

modified. The result of this growing acuteness of enemies has been, that

those mimics that now survive exhibit, as Mr. Bates well remarks, "a

palpably intentional likeness that is perfectly staggering," and also

"that those features of the portrait are most attended to by nature

which produce the most effective deception when the insects are seen in

nature." No one, in fact, can understand the perfection of the imitation

who has not seen these species in their native wilds. So complete is it

in general effect that in almost every box of butterflies, brought from

tropical America by amateurs, are to be found some species of the

mimicking Pieridae, Erycinidae, or moths, and the mimicked Heliconidae,

placed together under the impression that they are the same species. Yet

more extraordinary, it sometimes deceives the very insects themselves.

Mr. Trimen states that the male Danais chrysippus is sometimes deceived

by the female Diadema bolina which mimics that species. Dr. Fritz

MÃ¼ller, writing from Brazil to Professor Meldola, says, "One of the most

interesting of our mimicking butterflies is Leptalis melite. The female

alone of this species imitates one of our common white Pieridae, which

she copies so well that even her own male is often deceived; for I have

repeatedly seen the male pursuing the mimicked species, till, after

closely approaching and becoming aware of his error, he suddenly

returned."[100] This is evidently not a case of true mimicry, since the

species imitated is not protected; but it may be that the less abundant

Leptalis is able to mingle with the female Pieridae and thus obtain

partial immunity from attack. Mr. Kirby of the insect department of the

British Museum informs me that there are several species of South

American Pieridae which the female Leptalis melite very nearly

resembles. The case, however, is interesting as showing that the

butterflies are themselves deceived by a resemblance which is not so

great as that of some mimicking species.

\_Other Examples of Mimicry among Lepidoptera.\_

In tropical Asia, and eastward to the Pacific Islands, the Danaidae take

the place of the Heliconidae of America, in their abundance, their

conspicuousness, their slow flight, and their being the subjects of

mimicry. They exist under three principal forms or genera. The genus

Euploea is the most abundant both in species and individuals, and

consists of fine broad-winged butterflies of a glossy or metallic

blue-black colour, adorned with pure white, or rich blue, or dusky

markings situated round the margins of the wings. Danais has generally

more lengthened wings, of a semitransparent greenish or a rich brown

colour, with radial or marginal pale spots; while the fine Hestias are

of enormous size, of a papery or semitransparent white colour, with

dusky or black spots and markings. Each of these groups is mimicked by

various species of the genus Papilio, usually with such accuracy that it

is impossible to distinguish them on the wing.[101] Several species of

Diadema, a genus of butterflies allied to our Vanessas, also mimic

species of Danais, but in this case the females only are affected, a

subject which will be discussed in another chapter.

Another protected group in the Eastern tropics is that of the beautiful

day-flying moths forming the family Agaristidae. These are usually

adorned with the most brilliant colours or conspicuous markings, they

fly slowly in forests among the butterflies and other diurnal insects,

and their great abundance sufficiently indicates their possession of

some distastefulness which saves them from attack. Under these

conditions we may expect to find other moths which are not so protected

imitating them, and this is the case. One of the common and wide-ranging

species (Opthalmis lincea), found in the islands from Amboyna to New

Ireland, is mimicked in a wonderful manner by one of the Liparidae (the

family to which our common "tussock" and "vapourer" moths belong). This

is a new species collected at Amboyna during the voyage of the

\_Challenger\_, and has been named Artaxa simulans. Both insects are

black, with the apex of the fore wings ochre coloured, and the outer

half of the hind wings bright orange. The accompanying woodcuts (for the

use of which I am indebted to Mr. John Murray of the \_Challenger\_

Office) well exhibit their striking resemblance to each other.

[Illustration: FIG. 24.--Opthalmis lincea (Agaristidae). Artaxa simulans

(Liparidae).]

In Africa exactly similar phenomena recur, species of Papilio and of

Diadema mimicking Danaidae or Acraeidae with the most curious accuracy.

Mr. Trimen, who studied this subject in South Africa, has recorded eight

species or varieties of Diadema, and eight of Papilio, which each mimic

some species of Danais; while eight species or varieties of Panopaea

(another genus of Nymphalidae), three of Melanitis (Eurytelidae), and

two of Papilio, resemble with equal accuracy some species of

Acraea.[102] He has also independently observed the main facts on which

the explanation of the phenomenon rests,--the unpleasant odour of the

Danais and Acraea, extending to their larvae and pupae; their great

abundance, slow flight, and disregard of concealment; and he states that

while lizards, mantidae, and dragonflies all hunt butterflies, and the

rejected wings are to be found abundantly at some of their

feeding-places, those of the two genera Danais and Acraea were never

among them.

The two groups of the great genus Papilio (the true swallow-tailed

butterflies) which have been already referred to as having the special

characteristics of uneatable insects, have also their imitators in other

groups; and thus, the belief in their inedibility--derived mainly from

their style of warning coloration and their peculiar habits--is

confirmed. In South America, several species of the "Aeneas" group of

these butterflies are mimicked by Pieridae and by day-flying moths of

the genera Castnia and Pericopis. In the East, Papilio hector, P.

diphilus, and P. liris, all belonging to the inedible group, are

mimicked by the females of other species of Papilio belonging to very

distinct groups; while in Northern India and China, many fine day-flying

moths (Epicopeia) have acquired the strange forms and peculiar colours

of some of the large inedible Papilios of the same regions.

In North America, the large and handsome Danais archippus, with rich

reddish-brown wings, is very common; and it is closely imitated by

Limenitis misippus, a butterfly allied to our "white admiral," but which

has acquired a colour quite distinct from that of the great bulk of its

allies. In the same country there is a still more interesting case. The

beautiful dark bronzy green butterfly, Papilio philenor, is inedible

both in larva and perfect insect, and it is mimicked by the equally dark

Limenitis ursula. There is also in the Southern and Western States a

dark female form of the yellow Papilio turnus, which in all probability

obtains protection from its general resemblance to P. philenor. Mr. W.H.

Edwards has found, by extensive experiment, that both the dark and

yellow females produce their own kinds, with very few exceptions; and he

thinks that the dark form has the advantage in the more open regions and

in the prairies, where insectivorous birds abound. But in open country

the dark form would be quite as conspicuous as the yellow form, if not

more so, so that the resemblance to an inedible species would be there

more needed.[103]

The only probable case of mimicry in this country is that of the moth,

Diaphora mendica, whose female only is white, while the larva is of

protective colours, and therefore almost certainly edible. A much more

abundant moth, of about the same size and appearing about the same time,

is Spilosoma menthrasti, also white, but in this case both it and its

larva have been proved to be inedible. The white colour of the female

Diaphora, although it must be very conspicuous at night, may, therefore,

have been acquired in order to resemble the uneatable Spilosoma, and

thus gain some protection.[104]

\_Mimicry among Protected (Uneatable) Genera.\_

Before giving some account of the numerous other cases of warning

colours and of mimicry that occur in the animal kingdom, it will be well

to notice a curious phenomenon which long puzzled entomologists, but

which has at length received a satisfactory explanation.

We have hitherto considered, that mimicry could only occur when a

comparatively scarce and much persecuted species obtained protection by

its close external resemblance to a much more abundant uneatable species

inhabiting its own district; and this rule undoubtedly prevails among

the great majority of mimicking species all over the world. But Mr.

Bates also found a number of pairs of species of different genera of

Heliconidae, which resembled each other quite as closely as did the

other mimicking species he has described; and since all these insects

appear to be equally protected by their inedibility, and to be equally

free from persecution, it was not easy to see why this curious

resemblance existed, or how it had been brought about. That it is not

due to close affinity is shown by the fact that the resemblance occurs

most frequently between the two distinct sub-families into which (as Mr.

Bates first pointed out) the Heliconidae are naturally divided on

account of very important structural differences. One of these

sub-families (the true Heliconinae) consists of two genera only,

Heliconius and Eueides, the other (the Danaoid Heliconinae) of no less

than sixteen genera; and, in the instances of mimicry we are now

discussing, one of the pairs or triplets that resemble each other is

usually a species of the large and handsome genus Heliconius, the others

being species of the genera Mechanitis, Melinaea, or Tithorea, though

several species of other Danaoid genera also imitate each other. The

following lists will give some idea of the number of these curious

imitative forms, and of their presence in every part of the Neotropical

area. The bracketed species are those that resemble each other so

closely that the difference is not perceptible when they are on the

wing.

In the Lower Amazon region are found--

{ Heliconius sylvana.

{ Melinaea egina.

{ Heliconius numata.

{ Melinaea mneme.

{ Tithorea harmonia.

{ Methona psidii.

{ Thyridia ino.

{ Ceratina ninonia.

{ Melinaea mnasias.

In Central America are found--

{ Heliconius zuleika.

Nicaragua { Melinaea hezia.

{ Mechanitis sp.

{ Heliconius formosus.

{ Tithorea penthias.

Guatemala { Heliconius telchina.

{ Melinaea imitata.

In the Upper Amazon region--

{ Heliconius pardalinus.

{ Melinaea pardalis.

{ Heliconius aurora.

{ Melinaea lucifer.

In New Grenada--

{ Heliconius ismenius.

{ Melinaea messatis.

{ Heliconius messene.

{ Melinaea mesenina.

{ (?) Mechanitis sp.

{ Heliconius hecalesia.

{ Tithorea hecalesina.

{ Heliconius hecuba.

{ Tithorea bonplandi.

In Eastern Peru and Bolivia--

{ Heliconius aristona.

{ Melinaea cydippe.

{ (?) Mechanitis mothone.

In Pernambuco--

{ Heliconius ethra.

{ Mechanitis nesaea.

In Rio Janeiro--

{ Helieonius eucrate.

{ Mechanitis lysimnia.

In South Brazil--

{ Thyridia megisto.

{ Ituna ilione.

{ Acraea thalia.

{ Eueides pavana.

Besides these, a number of species of Ithomia and Napeogenes, and of

Napeogenes and Mechanitis, resemble each other with equal accuracy, so

that they are liable to be mistaken for each other when on the wing; and

no doubt many other equally remarkable cases are yet unnoticed.

[Illustration: FIG. 25.--Wings of Ituna Ilione, female. Wings of

Thyridia megisto, female.]

The figures above of the fore and hind wings of two of these mimicking

species, from Dr. Fritz MÃ¼ller's original paper in \_Kosmos\_, will serve

to show the considerable amount of difference, in the important

character of the neuration of the wings, between these butterflies,

which really belong to very distinct and not at all closely allied

genera. Other important characters are--(1) The existence of a small

basal cell in the hind wings of Ituna which is wanting in Thyridia; (2)

the division of the cell between the veins 1\_b\_ and 2 of the hind wings

in the former genus, while it is undivided in the latter; and (3) the

existence in Thyridia of scent-producing tufts of hair on the upper edge

of the hind wing, while in Ituna these are wanting; but in place of them

are extensible processes at the end of the abdomen, also emitting a

powerful scent. These differences characterise two marked subdivisions

of the Danaoid Heliconinae, each containing several distinct genera; and

these subdivisions are further distinguished by very different forms of

larvae, that to which Ituna belongs having from two to four long

threadlike tentacles on the back, while in that containing Thyridia

these are always absent. The former usually feed on Asclepiadeae, the

latter on Solanaceae or Scrophulariaceae.

The two species figured, though belonging to such distinct and even

remote genera, have acquired almost identical tints and markings so as

to be deceptively alike. The surface of the wings is, in both,

transparent yellowish, with black transverse bands and white marginal

spots, while both have similar black-and white-marked bodies and long

yellow antennae. Dr. MÃ¼ller states that they both show a preference for

the same flowers growing on the edges of the forest paths.[105]

We will now proceed to give the explanation of these curious

similarities, which have remained a complete puzzle for twenty years.

Mr. Bates, when first describing them, suggested that they might be due

to some form of parallel variation dependent on climatic influences; and

I myself adduced other cases of coincident local modifications of

colour, which did not appear to be explicable by any form of

mimicry.[106] But we neither of us hit upon the simple explanation given

by Dr. Fritz MÃ¼ller in 1879.

His theory is founded on the assumed, but probable, fact, that

insect-eating birds only learn by experience to distinguish the edible

from the inedible butterflies, and in doing so necessarily sacrifice a

certain number of the latter. The quantity of insectivorous birds in

tropical America is enormous; and the number of young birds which every

year have to learn wisdom by experience, as regards the species of

butterflies to be caught or to be avoided, is so great that the

sacrifice of life of the inedible species must be considerable, and, to

a comparatively weak or scarce species, of vital importance. The number

thus sacrificed will be fixed by the quantity of young birds, and by the

number of experiences requisite to cause them to avoid the inedible

species for the future, and not at all by the numbers of individuals of

which each species consists. Hence, if two species are so much alike as

to be mistaken for one another, the fixed number annually sacrificed by

inexperienced birds will be divided between them, and both will benefit.

But if the two species are very unequal in numbers, the benefit will be

comparatively slight for the more abundant species, but very great for

the rare one. To the latter it may make all the difference between

safety and destruction.

To give a rough numerical example. Let us suppose that in a given

limited district there are two species of Heliconidae, one consisting of

only 1000, the other of 100,000 individuals, and that the quota required

annually in the same district for the instruction of young insectivorous

birds is 500. By the larger species this loss will be hardly felt; to

the smaller it will mean the most dreadful persecution resulting in a

loss of half the total population. But, let the two species become

superficially alike, so that the birds see no difference between them.

The quota of 500 will now be taken from a combined population of 101,000

butterflies, and if proportionate numbers of each suffer, then the weak

species will only lose five individuals instead of 500 as it did before.

Now we know that the different species of Heliconidae are not equally

abundant, some being quite rare; so that the benefit to be derived in

these latter cases would be very important. A slight inferiority in

rapidity of flight or in powers of eluding attack might also be a cause

of danger to an inedible species of scanty numbers, and in this case too

the being merged in another much more abundant species, by similarity

of external appearance, would be an advantage.

The question of fact remains. Do young birds pursue and capture these

distasteful butterflies till they have learned by bitter experience what

species to avoid? On this point Dr. MÃ¼ller has fortunately been able to

obtain some direct evidence, by capturing several Acraeas and

Heliconidae which had evidently been seized by birds but had afterwards

escaped, as they had pieces torn out of the wing, sometimes

symmetrically out of both wings, showing that the insect had been seized

when at rest and with the two pairs of wings in contact. There is,

however, a general impression that this knowledge is hereditary, and

does not need to be acquired by young birds; in support of which view

Mr. Jenner Weir states that his birds always disregarded inedible

caterpillars. When, day by day, he threw into his aviary various larvae,

those which were edible were eaten immediately, those which were

inedible were no more noticed than if a pebble had been thrown before

the birds.

The cases, however, are not strictly comparable. The birds were not

young birds of the first year; and, what is more important, edible

larvae have a comparatively simple coloration, being always brown or

green and smooth. Uneatable larvae, on the other hand, comprise all that

are of conspicuous colours and are hairy or spiny. But with butterflies

there is no such simplicity of contrast. The eatable butterflies

comprise not only brown or white species, but hundreds of Nymphalidae,

Papilionidae, Lycaenidae, etc., which are gaily coloured and of an

immense variety of patterns. The colours and patterns of the inedible

kinds are also greatly varied, while they are often equally gay; and it

is quite impossible to suppose that any amount of instinct or inherited

habit (if such a thing exists) could enable young insectivorous birds to

distinguish all the species of one kind from all those of the other.

There is also some evidence to show that animals do learn by experience

what to eat and what to avoid. Mr. Poulton was assured by Rev. G.J.

Bursch that very young chickens peck at insects which they afterwards

avoid. Lizards, too, often seized larvae which they were unable to eat

and ultimately rejected.

Although the Heliconidae present, on the whole, many varieties of

coloration and pattern, yet, in proportion to the number of distinct

species in each district, the types of coloration are few and very well

marked, and thus it becomes easier for a bird or other animal to learn

that all belonging to such types are uneatable. This must be a decided

advantage to the family in question, because, not only do fewer

individuals of each species need to be sacrificed in order that their

enemies may learn the lesson of their inedibility, but they are more

easily recognised at a distance, and thus escape even pursuit. There is

thus a kind of mimicry between closely allied species as well as between

species of distinct genera, all tending to the same beneficial end. This

may be seen in the four or five distinct species of the genus Heliconius

which all have the same peculiar type of coloration--a yellow band

across the upper wings and radiating red stripes on the lower,--and are

all found in the same forests of the Lower Amazon; in the numerous very

similar species of Ithomia with transparent wings, found in every

locality of the same region; and in the very numerous species of Papilio

of the "Aeneas" group, all having a similar style of marking, the

resemblance being especially close in the females. The very uniform type

of colouring of the blue-black Euplaeas and of the fulvous Acraeas is of

the same character.[107] In all these cases the similarity of the allied

species is so great, that, when they are on the wing at some distance

off, it is difficult to distinguish one species from another. But this

close external resemblance is not always a sign of very near affinity;

for minute examination detects differences in the form and scalloping of

the wings, in the markings on the body, and in those on the under

surface of the wings, which do not usually characterise the closest

allies. It is to be further noted, that the presence of groups of very

similar species of the same genus, in one locality, is not at all a

common phenomenon among unprotected groups. Usually the species of a

genus found in one locality are each well marked and belong to somewhat

distinct types, while the closely allied forms--those that require

minute examination to discriminate them as distinct species--are most

generally found in separate areas, and are what are termed

representative forms.

The extension we have now given to the theory of mimicry is important,

since it enables us to explain a much wider range of colour phenomena

than those which were first imputed to mimicry. It is in the richest

butterfly region in the world--the Amazon valley--that we find the most

abundant evidence of the three distinct sets of facts, all depending on

the same general principle. The form of mimicry first elucidated by Mr.

Bates is characterised by the presence in each locality of certain

butterflies, or other insects, themselves edible and belonging to edible

groups, which derived protection from having acquired a deceptive

resemblance to some of the inedible butterflies in the same localities,

which latter were believed to be wholly free from the attacks of

insectivorous birds. Then came the extension of the principle, by Dr. F.

MÃ¼ller, to the case of species of distinct genera of the inedible

butterflies resembling each other quite as closely as in the former

cases, and like them always found in the same localities. They derive

mutual benefit from becoming, in appearance, one species, from which a

certain toll is taken annually to teach the young insectivorous birds

that they are uneatable. Even when the two or more species are

approximately equal in numbers, they each derive a considerable benefit

from thus combining their forces; but when one of the species is scarce

or verging on extinction, the benefit becomes exceedingly great, being,

in fact, exactly apportioned to the need of the species.

The third extension of the same principle explains the grouping of

allied species of the same genera of inedible butterflies into sets,

each having a distinct type of coloration, and each consisting of a

number of species which can hardly be distinguished on the wing. This

must be useful exactly in the same way as in the last case, since it

divides the inevitable toll to insectivorous birds and other animals

among a number of species. It also explains the fact of the great

similarity of many species of inedible insects in the same locality--a

similarity which does not obtain to anything like the same extent among

the edible species. The explanation of the various phenomena of

resemblance and mimicry, presented by the distasteful butterflies, may

now be considered tolerably complete.

\_Mimicry in other Orders of Insects.\_

A very brief sketch of these phenomena will be given, chiefly to show

that the same principle prevails throughout nature, and that, wherever a

rather extensive group is protected, either by distastefulness or

offensive weapons, there are usually some species of edible and

inoffensive groups that gain protection by imitating them. It has been

already stated that the Telephoridae, Lampyridae, and other families of

soft-winged beetles, are distasteful; and as they abound in all parts of

the world, and especially in the tropics, it is not surprising that

insects of many other groups should imitate them. This is especially the

case with the longicorn beetles, which are much persecuted by

insectivorous birds; and everywhere in tropical regions some of these

are to be found so completely disguised as to be mistaken for species of

the protected groups. Numbers of these imitations have been already

recorded by Mr. Bates and myself, but I will here refer to a few others.

In the recently published volumes on the Longicorn and Malacoderm

beetles of Central America[108] there are numbers of beautifully

coloured figures of the new species; and on looking over them we are

struck by the curious resemblance of some of the Longicorns to species

of the Malacoderm group. In some cases we discover perfect mimics, and

on turning to the descriptions we always find these pairs to come from

the same locality. Thus the Otheostethus melanurus, one of the

Prionidae, imitates the malacoderm, Lucidota discolor, in form, peculiar

coloration, and size, and both are found at Chontales in Nicaragua, the

species mimicked having, however, as is usual, a wider range. The

curious and very rare little longicorn, Tethlimmena aliena, quite unlike

its nearest allies in the same country, is an exact copy on a somewhat

smaller scale of a malacoderm, Lygistopterus amabilis, both found at

Chontales. The pretty longicorn, Callia albicornis, closely resembles

two species of malacoderms (Silis chalybeipennis and Colyphus

signaticollis), all being small beetles with red head and thorax and

bright blue elytra, and all three have been found at Panama. Many other

species of Callia also resemble other malacoderms; and the longicorn

genus Lycidola has been named from its resemblance to various species of

the Lycidae, one of the species here figured (Lycidola belti) being a

good mimic of Calopteron corrugatum and of several other allied species,

all being of about the same size and found at Chontales. In these cases,

and in most others, the longicorn beetles have lost the general form and

aspect of their allies to take on the appearance of a distinct tribe.

Some other groups of beetles, as the Elateridae and Eucnemidae, also

deceptively mimic malacoderms.

Wasps and bees are often closely imitated by insects of other orders.

Many longicorn beetles in the tropics exactly mimic wasps, bees, or

ants. In Borneo a large black wasp, whose wings have a broad white patch

near the apex (Mygnimia aviculus), is closely imitated by a heteromerous

beetle (Coloborhombus fasciatipennis), which, contrary to the general

habit of beetles, keeps its wings expanded in order to show the white

patch on their apex, the wing-coverts being reduced to small oval

scales, as shown in the figure. This is a most remarkable instance of

mimicry, because the beetle has had to acquire so many characters which

are unknown among its allies (except in another species from Java)--the

expanded wings, the white band on them, and the oval scale-like

elytra.[109] Another remarkable case has been noted by Mr. Neville

Goodman, in Egypt, where a common hornet (Vespa orientalis) is exactly

imitated in colour, size, shape, attitude when at rest, and mode of

flight, by a beetle of the genus Laphria.[110]

The tiger-beetles (Cicindelidae) are also the subjects of mimicry by

more harmless insects. In the Malay Islands I found a heteromerous

beetle which exactly resembled a Therates, both being found running on

the trunks of trees. A longicorn (Collyrodes Lacordairei) mimics

Collyris, another genus of the same family; while in the Philippine

Islands there is a cricket (Condylodeira tricondyloides), which so

closely resembles a tiger-beetle of the genus Tricondyla that the

experienced entomologist, Professor Westwood, at first placed it in his

cabinet among those beetles.

[Illustration: FIG. 26.--Mygnimia aviculus (Wasp). Coloborhombus

fasciatipennis (Beetle).]

[Illustration: FIG. 27.

a. Doliops sp. (Longicorn)

mimics Pachyrhynchus orbifae, (b) (a hard curculio).

c. Doliops curculionoides mimics (d) Pachyrhynchus sp.

e. Scepastus pachyrhynchoides (a grasshopper),

mimics (f) Apocyrtus sp. (a hard curculio).

g. Doliops sp. mimics (h) Pachyrhynchus sp.

i. Phoraspis (grasshopper) mimics (k) a Coccinella.

All the above are from the Philippines. The exact correspondence of the

colours of the insects themselves renders the mimicry much more complete

in nature than it appears in the above figures.]

One of the characters by which some beetles are protected is excessive

hardness of the elytra and integuments. Several genera of weevils

(Curculionidae) are thus saved from attack, and these are often mimicked

by species of softer and more eatable groups. In South America, the

genus Heilipus is one of these hard groups, and both Mr. Bates and M.

Roelofs, a Belgian entomologist, have noticed that species of other

genera exactly mimic them. So, in the Philippines, there is a group of

Curculionidae, forming the genus Pachyrhynchus, in which all the species

are adorned with the most brilliant metallic colours, banded and spotted

in a curious manner, and are very smooth and hard. Other genera of

Curculionidae (Desmidophorus, Alcides), which are usually very

differently coloured, have species in the Philippines which mimic the

Pachyrhynchi; and there are also several longicorn beetles (Aprophata,

Doliops, Acronia, and Agnia), which also mimic them. Besides these,

there are some longicorns and cetonias which reproduce the same colours

and markings; and there is even a cricket (Scepastus pachyrhynchoides),

which has taken on the form and peculiar coloration of these beetles in

order to escape from enemies, which then avoid them as uneatable.[111]

The figures on the opposite page exhibit several other examples of these

mimicking insects.

Innumerable other cases of mimicry occur among tropical insects; but we

must now pass on to consider a few of the very remarkable, but much

rarer instances, that are found among the higher animals.

\_Mimicry among the Vertebrata.\_

Perhaps the most remarkable cases yet known are those of certain

harmless snakes which mimic poisonous species. The genus Elaps, in

tropical America, consists of poisonous snakes which do not belong to

the viper family (in which are included the rattlesnakes and most of

those which are poisonous), and which do not possess the broad

triangular head which characterises the latter. They have a peculiar

style of coloration, consisting of alternate rings of red and black, or

red, black, and yellow, of different widths and grouped in various ways

in the different species; and it is a style of coloration which does not

occur in any other group of snakes in the world. But in the same regions

are found three genera of harmless snakes, belonging to other families,

some few species of which mimic the poisonous Elaps, often so exactly

that it is with difficulty one can be distinguished from the other. Thus

Elaps fulvius in Guatemala is imitated by the harmless Pliocerus

equalis; Elaps corallinus in Mexico is mimicked by the harmless

Homalocranium semicinctum; and Elaps lemniscatus in Brazil is copied by

Oxyrhopus trigeminus; while in other parts of South America similar

cases of mimicry occur, sometimes two harmless species imitating the

same poisonous snake.

A few other instances of mimicry in this group have been recorded. There

is in South Africa an egg-eating snake (Dasypeltis scaber), which has

neither fangs nor teeth, yet it is very like the Berg adder (Clothos

atropos), and when alarmed renders itself still more like by flattening

out its head and darting forward with a hiss as if to strike a foe.[112]

Dr. A.B. Meyer has also discovered that, while some species of the genus

Callophis (belonging to the same family as the American Elaps) have

large poison fangs, other species of the same genus have none; and that

one of the latter (C. gracilis) resembles a poisonous species (C.

intestinalis) so closely, that only an exact comparison will discover

the difference of colour and marking. A similar kind of resemblance is

said to exist between another harmless snake, Megaerophis flaviceps, and

the poisonous Callophis bivirgatus; and in both these cases the harmless

snake is less abundant than the poisonous one, as occurs in all examples

of true mimicry.[113]

In the genus Elaps, above referred to, the very peculiar style of colour

and marking is evidently a "warning colour" for the purpose of

indicating to snake-eating birds and mammals that these species are

poisonous; and this throws light on the long-disputed question of the

use of the rattle of the rattlesnake. This reptile is really both

sluggish and timid, and is very easily captured by those who know its

habits. If gently tapped on the head with a stick, it will coil itself

up and lie still, only raising its tail and rattling. It may then be

easily caught. This shows that the rattle is a warning to its enemies

that it is dangerous to proceed to extremities; and the creature has

probably acquired this structure and habit because it frequents open or

rocky districts where protective colour is needful to save it from being

pounced upon by buzzards or other snake-eaters. Quite parallel in

function is the expanded hood of the Indian cobra, a poisonous snake

which belongs also to the Elapidae. This is, no doubt, a warning to its

foes, not an attempt to terrify its prey; and the hood has been

acquired, as in the case of the rattlesnake, because, protective

coloration being on the whole useful, some mark was required to

distinguish it from other protectively coloured, but harmless, snakes.

Both these species feed on active creatures capable of escaping if their

enemy were visible at a moderate distance.

\_Mimicry among Birds.\_

The varied forms and habits of birds do not favour the production among

them of the phenomena of warning colours or of mimicry; and the extreme

development of their instincts and reasoning powers, as well as their

activity and their power of flight, usually afford them other means of

evading their enemies. Yet there are a few imperfect, and one or two

very perfect cases of true mimicry to be found among them. The less

perfect examples are those presented by several species of cuckoos, an

exceedingly weak and defenceless group of birds. Our own cuckoo is, in

colour and markings, very like a sparrow-hawk. In the East, several of

the small black cuckoos closely resemble the aggressive drongo-shrikes

of the same country, and the small metallic cuckoos are like glossy

starlings; while a large ground-cuckoo of Borneo (Carpococcyx radiatus)

resembles one of the fine pheasants (Euplocamus) of the same country,

both in form and in its rich metallic colours.

More perfect cases of mimicry occur between some of the dull-coloured

orioles in the Malay Archipelago and a genus of large honey-suckers--the

Tropidorhynchi or "Friar-birds." These latter are powerful and noisy

birds which go in small flocks. They have long, curved, and sharp beaks,

and powerful grasping claws; and they are quite able to defend

themselves, often driving away crows and hawks which venture to approach

them too nearly. The orioles, on the other hand, are weak and timid

birds, and trust chiefly to concealment and to their retiring habits to

escape persecution. In each of the great islands of the Austro-Malayan

region there is a distinct species of Tropidorhynchus, and there is

always along with it an oriole that exactly mimics it. All the

Tropidorhynchi have a patch of bare black skin round the eyes, and a

ruff of curious pale recurved feathers on the nape, whence their name of

Friar-birds, the ruff being supposed to resemble the cowl of a friar.

These peculiarities are imitated in the orioles by patches of feathers

of corresponding colours; while the different tints of the two species

in each island are exactly the same. Thus in Bouru both are earthy

brown; in Ceram they are both washed with yellow ochre; in Timor the

under surface is pale and the throat nearly white, and Mr. H.O. Forbes

has recently discovered another pair in the island of Timor Laut. The

close resemblance of these several pairs of birds, of widely different

families, is quite comparable with that of many of the insects already

described. It is so close that the preserved specimens have even

deceived naturalists; for, in the great French work, \_Voyage de

l'Astrolabe\_, the oriole of Bouru is actually described and figured as a

honey-sucker; and Mr. Forbes tells us that, when his birds were

submitted to Dr. Sclater for description, the oriole and the

honey-sucker were, previous to close examination, considered to be the

same species.

\_Objections to the Theory of Mimicry.\_

To set forth adequately the varied and surprising facts of mimicry would

need a large and copiously illustrated volume; and no more interesting

subject could be taken up by a naturalist who has access to our great

collections and can devote the necessary time to search out the many

examples of mimicry that lie hidden in our museums. The brief sketch of

the subject that has been here given will, however, serve to indicate

its nature, and to show the weakness of the objections that were at

first made to it. It was urged that the action of "like conditions,"

with "accidental resemblances" and "reversion to ancestral types," would

account for the facts. If, however, we consider the actual phenomena as

here set forth, and the very constant conditions under which they occur,

we shall see how utterly inadequate are these causes, either singly or

combined. These constant conditions are--

1. That the imitative species occur in the same area and occupy

the very same station as the imitated.

2. That the imitators are always the more defenceless.

3. That the imitators are always less numerous in individuals.

4. That the imitators differ from the bulk of their allies.

5. That the imitation, however minute, is \_external\_ and

\_visible\_ only, never extending to internal characters or to

such as do not affect the external appearance.

These five characteristic features of mimicry show us that it is really

an exceptional form of protective resemblance. Different species in the

same group of organisms may obtain protection in different ways: some by

a general resemblance to their environment; some by more exactly

imitating the objects that surround them--bark, or leaf, or flower;

while others again gain an equal protection by resembling some species

which, from whatever cause, is almost as free from attack as if it were

a leaf or a flower. This immunity may depend on its being uneatable, or

dangerous, or merely strong; and it is the resemblance to such creatures

for the purpose of sharing in their safety that constitutes mimicry.

\_Concluding Remarks on Warning Colours and Mimicry.\_

Colours which have been acquired for the purpose of serving as a warning

of inedibility, or of the possession of dangerous offensive weapons, are

probably more numerous than have been hitherto supposed; and, if so, we

shall be able to explain a considerable amount of colour in nature for

which no use has hitherto been conjectured. The brilliant and varied

colours of sea-anemones and of many coral animals will probably come

under this head, since we know that many of them possess the power of

ejecting stinging threads from various parts of their bodies which

render them quite uneatable to most animals. Mr. Gosse describes how, on

putting an Anthea into a tank containing a half-grown bullhead (Cottus

bubalis) which had not been fed for some time, the fish opened his mouth

and sucked in the morsel, but instantly shot it out again. He then

seized it a second time, and after rolling it about in his mouth for a

moment shot it out again, and then darted away to hide himself in a

hole. Some tropical fishes, however, of the genera Tetrodon,

Pseudoscarus, Astracion, and a few others, seem to have acquired the

power of feeding on corals and medusae; and the beautiful bands and

spots and bright colours with which they are frequently adorned, may be

either protective when feeding in the submarine coral groves, or may, in

some cases, be warning colours to show that they themselves are

poisonous and uneatable.

A remarkable illustration of the wide extension of warning colours, and

their very definite purpose in nature, is afforded by what may now be

termed "Mr. Belt's frog." Frogs in all parts of the world are, usually,

protectively coloured with greens or browns; and the little tree-frogs

are either green like the leaves they rest upon, or curiously mottled to

imitate bark or dead leaves. But there are a certain number of very

gaily coloured frogs, and these do not conceal themselves as frogs

usually do. Such was the small toad found by Darwin at Bahia Blanca,

which was intense black and bright vermilion, and crawled about in the

sunshine over dry sand-hills and arid plains. And in Nicaragua, Mr. Belt

found a little frog gorgeously dressed in a livery of red and blue,

which did not attempt concealment and was very abundant, a combination

of characters which convinced him that it was uneatable. He, therefore,

took a few specimens home with him and gave them to his fowls and ducks,

but none would touch them. At last, by throwing down pieces of meat, for

which there was a great competition among the poultry, he managed to

entice a young duck into snatching up one of the little frogs. Instead

of swallowing it, however, the duck instantly threw it out of its mouth,

and went about jerking its head as if trying to get rid of some

unpleasant taste.[114]

The power of predicting what will happen in a given case is always

considered to be a crucial test of a true theory, and if so, the theory

of warning colours, and with it that of mimicry, must be held to be well

established. Among the creatures which probably have warning colours as

a sign of inedibility are, the brilliantly coloured nudibranchiate

molluscs, those curious annelids the Nereis and the Aphrodite or

sea-mouse, and many other marine animals. The brilliant colours of the

scallops (Pecten) and some other bivalve shells are perhaps an

indication of their hardness and consequent inedibility, as in the case

of the hard beetles; and it is not improbable that some of the

phosphorescent fishes and other marine organisms may, like the

glow-worm, hold out their lamp as a warning to enemies.[115] In

Queensland there is an exceedingly poisonous spider, whose bite will

kill a dog, and cause severe illness with excruciating pain in man. It

is black, with a bright vermilion patch on the middle of the body; and

it is so well recognised by this conspicuous coloration that even the

spider-hunting wasps avoid it.[116]

Locusts and grasshoppers are generally of green protective tints, but

there are many tropical species most gaudily decorated with red, blue,

and black colours. On the same general grounds as those by which Mr.

Belt predicted the inedibility of his conspicuous frog, we might safely

predict the same for these insects; but we have fortunately a proof that

they are so protected, since Mr. Charles Home states that one of the

bright coloured Indian locusts was invariably rejected when offered to

birds and lizards.[117]

\* \* \* \* \*

The examples now given lead us to the conclusion that colours acquired

for the purpose of serving as a danger-signal to enemies are very

widespread in nature, and, with the corresponding colours of the species

which mimic them, furnish us with a rational explanation of a

considerable portion of the coloration of animals which is outside the

limits of those colours that have been acquired for either protection or

recognition. There remains, however, another set of colours, chiefly

among the higher animals, which, being connected with some of the most

interesting and most disputed questions in natural history, must be

discussed in a separate chapter.

FOOTNOTES:

[Footnote 92: \_Nature\_, vol. iii. p. 165. Professor Meldola observed

that specimens of Danais and Euplaea in collections were less subject to

the attacks of mites \_(Proc. Ent. Soc.\_, 1877, p. xii.); and this was

corroborated by Mr. Jenner Weir. \_Entomologist\_, 1882, vol. xv. p. 160.]

[Footnote 93: See Darwin's \_Descent of Man\_, p. 325.]

[Footnote 94: \_Transactions of the Entomological Society of London\_,

1869, p. 21.]

[Footnote 95: \_Ibid.\_, p. 27.]

[Footnote 96: \_Nature\_, vol. iii. p. 147.]

[Footnote 97: Stainton's \_Manual of Butterflies and Moths\_, vol. i. p.

93; E.B. Poulton, \_Proceedings of the Zool. Soc. of London\_, 1887, pp.

191-274.]

[Footnote 98: See \_Transactions of the Linnean Society\_, vol. xxiii. pp.

495-566, coloured plates.]

[Footnote 99: These butterflies are now divided into two sub-families,

one of which is placed with the Danaidae; but to avoid confusion I shall

always speak of the American genera under the old term Heliconidae.]

[Footnote 100: R. Meldola in \_Ann. and Mag. of Nat. Hist.\_, Feb. 1878,

p. 158.]

[Footnote 101: See \_Trans. Linn. Soc.\_, vol. xxv. Wallace, on Variation

of Malayan Papilionidae; and, Wallace's \_Contributions to Natural

Selection\_ chaps. iii. and iv., where full details are given.]

[Footnote 102: See \_Trans. Linn. Soc.\_, vol. xxvi., with two coloured

plates illustrating cases of mimicry.]

[Footnote 103: Edwards's \_Butterflies of North America\_, second series,

part vi.]

[Footnote 104: Professor Meldola informs me that he has recorded another

case of mimicry among British moths, in which Acidalia subsericata

imitates Asthena candidata. See \_Ent. Mo. Mag.\_, vol. iv. p. 163.]

[Footnote 105: From Professor Meldola's translation of Dr. F. MÃ¼ller's

paper, in \_Proc. Ent. Soc. Lond.\_, 1879, p. xx.]

[Footnote 106: \_Island Life\_, p. 255.]

[Footnote 107: This extension of the theory of mimicry was pointed out

by Professor Meldola in the paper already referred to; and he has

answered the objections to Dr. F. MÃ¼ller's theory with great force in

the \_Annals and Mag. of Nat. Hist.\_, 1882, p. 417.]

[Footnote 108: Godman and Salvin's \_Biologia Centrali-Americana,

Insecta, Coleoptera\_, vol. iii. part ii., and vol. v.]

[Footnote 109: \_Trans. Ent. Soc.\_, 1885, p. 369.]

[Footnote 110: \_Proc. Cambridge Phil. Soc.\_, vol. iii. part ii., 1877.]

[Footnote 111: \_Compte-Rendu de la SociÃ©tÃ© Entomologique de Belgaue\_,

series ii., No. 59, 1878.]

[Footnote 112: \_Nature\_, vol. xxxiv. p. 547.]

[Footnote 113: \_Proceedings of the Zool. Soc. of London\_, 1870, p. 369.]

[Footnote 114: \_The Naturalist in Nicaragua\_, p. 321.]

[Footnote 115: Mr. Belt first suggested this use of the light of the

Lampyridae (fireflies and glow-worms)--\_Naturalist in Nicaragua\_, p.

320. Mr. Verrill and Professor Meldola made the same suggestion in the

case of medusae and other phosphorescent marine organisms (\_Nature\_,

vol. xxx. pp. 281, 289).]

[Footnote 116: W.E. Armit, in \_Nature\_, vol. xviii. p. 642.]

[Footnote 117: \_Proc. Ent. Soc.\_, 1869, p. xiii.]

CHAPTER X

COLOURS AND ORNAMENTS CHARACTERISTIC OF SEX

Sex colours in the mollusca and crustacea--In insects--In

butterflies and moths--Probable causes of these colours--Sexual

selection as a supposed cause--Sexual coloration of birds--Cause

of dull colours of female birds--Relation of sex colour to

nesting habits--Sexual colours of other vertebrates--Sexual

selection by the struggles of males--Sexual characters due to

natural selection--Decorative plumage of males and its effect on

the females--Display of decorative plumage by the males--A

theory of animal coloration--The origin of accessory

plumes--Development of accessory plumes and their display--The

effect of female preference will be neutralised by natural

selection--General laws of animal coloration--Concluding

remarks.

In the preceding chapters we have dealt chiefly with the coloration of

animals as distinctive of the several species; and we have seen that, in

an enormous number of cases, the colours can be shown to have a definite

purpose, and to be useful either as a means of protection or

concealment, of warning to enemies, or of recognition by their own kind.

We have now to consider a subordinate but very widespread

phenomenon---the differences of colour or of ornamental appendages in

the two sexes. These differences are found to have special relations

with the three classes of coloration above referred to, in many cases

confirming the explanation already given of their purport and use, and

furnishing us with important aid in formulating a general theory of

animal coloration.

In comparing the colours of the two sexes we find a perfect gradation,

from absolute identity of colour up to such extreme difference that it

is difficult to believe that the two forms can belong to the same

species; and this diversity in the colours of the sexes does not bear

any constant relation to affinity or systematic position. In both

insects and birds we find examples of complete identity and extreme

diversity of the sexes; and these differences occur sometimes in the

same tribe or family, and sometimes even in the same genus.

It is only among the higher and more active animals that sexual

differences of colour acquire any prominence. In the mollusca the two

sexes, when separated, are always alike in colour, and only very rarely

present slight differences in the form of the shell. In the extensive

group of crustacea the two sexes as a rule are identical in colour,

though there are often differences in the form of the prehensile organs;

but in a very few cases there are differences of colour also. Thus, in a

Brazilian species of shore-crab (Gelasimus) the female is grayish-brown,

while in the male the posterior part of the cephalo-thorax is pure

white, with the anterior part of a rich green. This colour is only

acquired by the males when they become mature, and is liable to rapid

change in a few minutes to dusky tints.[118] In some of the freshwater

fleas (Daphnoidae) the males are ornamented with red and blue spots,

while in others similar colours occur in both sexes. In spiders also,

though as a rule the two sexes are alike in colour, there are a few

exceptions, the males being ornamented with brilliant colours on the

abdomen, while the female is dull coloured.

\_Sexual Coloration in Insects.\_

It is only when we come to the winged insects that we find any large

amount of peculiarity in sexual coloration, and even here it is only

developed in certain orders. Flies (Diptera), field-bugs (Hemiptera),

cicadas (Homoptera), and the grasshoppers, locusts, and crickets

(Orthoptera) present very few and unimportant sexual differences of

colour; but the last two groups have special musical organs very fully

developed in the males of some of the species, and these no doubt enable

the sexes to discover and recognise each other. In some cases, however,

when the female is protectively coloured, as in the well-known

leaf-insects already referred to (p. 207), the male is smaller and much

less protectively formed and coloured. In the bees and wasps

(Hymenoptera) it is also the rule that the sexes are alike in colour,

though there are several cases among solitary bees where they differ;

the female being black, and the male brown in Anthophora retusa, while

in Andraena fulva the female is more brightly coloured than the male. Of

the great order of beetles (Coleoptera) the same thing may be said.

Though often so rich and varied in their colours the sexes are usually

alike, and Mr. Darwin was only able to find about a dozen cases in which

there was any conspicuous difference between them.[119] They exhibit,

however, numerous sexual characters, in the length of the antennae, and

in horns, legs, or jaws remarkably enlarged or curiously modified in the

male sex.

It is in the family of dragonflies (order Neuroptera) that we first meet

with numerous cases of distinctive sexual coloration. In some of the

Agrionidae the males have the bodies rich blue and the wings black,

while the females have the bodies green and the wings transparent. In

the North American genus Hetaerina the males alone have a carmine spot

at the base of each wing; but in some other genera the sexes hardly

differ at all.

The great order of Lepidoptera, including the butterflies and moths,

affords us the most numerous and striking examples of diversity of

sexual colouring. Among the moths the difference is usually but slight,

being manifested in a greater intensity of the colour of the smaller

winged male; but in a few cases there is a decided difference, as in the

ghost-moth (Hepialus humuli), in which the male is pure white, while the

female is yellow with darker markings. This may be a recognition colour,

enabling the female more readily to discover her mate; and this view

receives some support from the fact that in the Shetland Islands the

male is almost as yellow as the female, since it has been suggested that

at midsummer, when this moth appears, there is in that high latitude

sufficient twilight all night to render any special coloration

unnecessary.[120]

Butterflies present us with a wonderful amount of sexual difference of

colour, in many cases so remarkable that the two sexes of the same

species remained for many years under different names and were thought

to be quite distinct species. We find, however, every gradation from

perfect identity to complete diversity, and in some cases we are able to

see a reason for this difference. Beginning with the most extraordinary

cases of diversity--as in Diadema misippus, where the male is black,

ornamented with a large white spot on each wing margined with rich

changeable blue, while the female is orange-brown with black spots and

stripes--we find the explanation in the fact that the female mimics an

uneatable Danais, and thus gains protection while laying its eggs on low

plants in company with that insect. In the allied species, Diadema

bolina, the females are also very different from the males, but are of

dusky brown tints, evidently protective and very variable, some

specimens having a general resemblance to the uneatable Euplaeas; so

that we see here some of the earlier stages of both forms of protection.

The remarkable differences in some South American Pieridae are similarly

explained. The males of Pieris pyrrha, P. lorena, and several others,

are white with a few black bands and marginal spots like so many of

their allies, while the females are gaily coloured with yellow and

brown, and exactly resemble some species of the uneatable Heliconidae of

the same district. Similarly, in the Malay Archipelago, the female of

Diadema anomala is glossy metallic blue, while the male is brown; the

reason for this reversal of the usual rule being, that the female

exactly mimics the brilliant colouring of the common and uneatable

Euplaea midamus, and thus secures protection. In the fine Adolias

dirtea, the male is black with a few specks of ochre-yellow and a broad

marginal band of rich metallic greenish-blue, while the female is

brownish-black entirely covered with rows of ochre-yellow spots. This

latter coloration does not appear to be protective when the insect is

seen in the cabinet, but it really is so. I have observed the female of

this butterfly in Sumatra, where it settles on the ground in the forest,

and its yellow spots so harmonise with the flickering gleams of sunlight

on the dead leaves that it can only be detected with the greatest

difficulty.

A hundred other cases might be quoted in which the female is either

more obscurely coloured than the male, or gains protection by imitating

some inedible species; and any one who has watched these female insects

flying slowly along in search of the plants on which to deposit their

eggs, will understand how important it must be to them not to attract

the attention of insect-eating birds by too conspicuous colours. The

number of birds which capture insects on the wing is much greater in

tropical regions than in Europe; and this is perhaps the reason why many

of our showy species are alike, or almost alike, in both sexes, while

they are protectively coloured on the under side which is exposed to

view when they are at rest. Such are our peacock, tortoise-shell, and

red admiral butterflies; while in the tropics we more commonly find that

the females are less conspicuous on the upper surface even when

protectively coloured beneath.

We may here remark, that the cases already quoted prove clearly that

either male or female may be modified in colour apart from the opposite

sex. In Pieris pyrrha and its allies the male retains the usual type of

coloration of the whole genus, while the female has acquired a distinct

and peculiar style of colouring. In Adolias dirtea, on the other hand,

the female appears to retain something like the primitive colour and

markings of the two sexes, modified perhaps for more perfect protection;

while the male has acquired more and more intense and brilliant colours,

only showing his original markings by the few small yellow spots that

remain near the base of the wings. In the more gaily coloured Pieridae,

of which our orange-tip butterfly may be taken as a type, we see in the

female the plain ancestral colours of the group, while the male has

acquired the brilliant orange tip to its wings, probably as a

recognition mark.

In those species in which the under surface is protectively coloured, we

often find the upper surface alike in both sexes, the tint of colour

being usually more intense in the male. But in some cases this leads to

the female being more conspicuous, as in some of the Lycaenidae, where

the female is bright blue and the male of a blue so much deeper and

soberer in tint as to appear the less brilliantly coloured of the two.

\_Probable Causes of these Colours.\_

In the production of these varied results there have probably been

several causes at work. There seems to be a constant tendency in the

male of most animals--but especially of birds and insects--to develop

more and more intensity of colour, often culminating in brilliant

metallic blues or greens or the most splendid iridescent hues; while, at

the same time, natural selection is constantly at work, preventing the

female from acquiring these same tints, or modifying her colours in

various directions to secure protection by assimilating her to her

surroundings, or by producing mimicry of some protected form. At the

same time, the need for recognition must be satisfied; and this seems to

have led to diversities of colour in allied species, sometimes the

female, sometimes the male undergoing the greatest change according as

one or other could be modified with the greatest ease, and so as to

interfere least with the welfare of the race. Hence it is that sometimes

the males of allied species vary most, as in the different species of

Epicalia; sometimes the females, as in the magnificent green species of

Ornithoptera and the "Aeneas" group of Papilio.

The importance of the two principles--the need of protection and

recognition--in modifying the comparative coloration of the sexes among

butterflies, is beautifully illustrated in the case of the groups which

are protected by their distastefulness, and whose females do not,

therefore, need the protection afforded by sober colours.

In the great families, Heliconidae and Acraeidae, we find that the two

sexes are almost always alike; and, in the very few exceptions, that the

female, though differently, is not less gaily or less conspicuously

coloured. In the Danaidae the same general rule prevails, but the cases

in which the male exhibits greater intensity of colour than the female

are perhaps more numerous than in the other two families. There is,

however, a curious difference in this respect between the Oriental and

the American groups of distasteful Papilios with warning colours, both

of which are the subjects of mimicry. In the Eastern groups--of which P.

hector and P. coon may be taken as types--the two sexes are nearly

alike, the male being sometimes more intensely coloured and with fewer

pale markings; but in the American groups--represented by P. aeneas, P.

sesostris, and allies--there is a wonderful diversity, the males having

a rich green or bluish patch on the fore wings, while the females have a

band or spots of pure white, not always corresponding in position to the

green spot of the males. There are, however, transitional forms, by

which a complete series can be traced, from close similarity to great

diversity of colouring between the sexes; and this may perhaps be only

an extreme example of the intenser colour and more concentrated markings

which are a very prevalent characteristic of male butterflies.

There are, in fact, many indications of a regular succession of tints in

which colour development has occurred in the various groups of

butterflies, from an original grayish or brownish neutral tint. Thus in

the "Aeneas" group of Papilios we have the patch on the upper wings

yellowish in P. triopas, olivaceous in P. bolivar, bronzy-gray with a

white spot in P. erlaces, more greenish and buff in P. iphidamas,

gradually changing to the fine blue of P. brissonius, and the

magnificent green of P. sesostris. In like manner, the intense crimson

spots of the lower wings can be traced step by step from a yellow or

buff tint, which is one of the most widespread colours in the whole

order. The greater purity and intensity of colour seem to be usually

associated with more pointed wings, indicating greater vigour and more

rapid flight.

\_Sexual Selection as a supposed Cause of Colour Development.\_

Mr. Darwin, as is well known, imputed most of the brilliant colours and

varied patterns of butterflies' wings to sexual selection--that is, to a

constant preference, by female butterflies, for the more brilliant

males; the colours thus produced being sometimes transmitted to the

males alone, sometimes to both sexes. This view has always seemed to me

to be unsupported by evidence, while it is also quite inadequate to

account for the facts. The only direct evidence, as set forth with his

usual fairness by Mr. Darwin himself, is opposed to his views. Several

entomologists assured him that, in moths, the females evince not the

least choice of their partners; and Dr. Wallace of Colchester, who has

largely bred the fine Bombyx cynthia, confirmed this statement. Among

butterflies, several males often pursue one female, and Mr. Darwin says,

that, unless the female exerts a choice the pairing must be left to

chance. But, surely, it may be the most vigorous or most persevering

male that is chosen, not necessarily one more brightly or differently

coloured, and this will be true "natural selection." Butterflies have

been noticed to prefer some coloured flowers to others; but that does

not prove, or even render probable, any preference for the colour

itself, but only for flowers of certain colours, on account of the more

agreeable or more abundant nectar obtained from them. Dr. Schulte called

Mr. Darwin's attention to the fact, that in the Diadema bolina the

brilliant blue colour surrounding the white spots is only visible when

we look towards the insect's head, and this is true of many of the

iridescent colours of butterflies, and probably depends upon the

direction of the striae on the scales. It is suggested, however, that

this display of colour will be seen by the female as the male is

approaching her, and that it has been developed by sexual

selection.[121] But in the majority of cases the males \_follow\_ the

female, hovering over her in a position which would render it almost

impossible for her to see the particular colours or patterns on his

upper surface; to do so the female should mount higher than the male,

and fly towards him--being the seeker instead of the sought, and this is

quite opposed to the actual facts. I cannot, therefore, think that this

suggestion adds anything whatever to the evidence for sexual selection

of colour by female butterflies. This question will, however, be again

touched upon after we have considered the phenomena of sexual colour

among the vertebrata.

\_Sexual Coloration of Birds.\_

The general rule among vertebrates, as regards colour, is, for the two

sexes to be alike. This prevails, with only a few exceptions, in fishes,

reptiles, and mammalia; but in birds diversity of sexual colouring is

exceedingly frequent, and is, not improbably, present in a greater or

less degree in more than half of the known species. It is this class,

therefore, that will afford us the best materials for a discussion of

the problem, and that may perhaps lead us to a satisfactory explanation

of the causes to which sexual colour is due.

The most fundamental characteristic of birds, from our present point of

view, is a greater intensity of colour in the male. This is the case in

hawks and falcons; in many thrushes, warblers, and finches; in pigeons,

partridges, rails, plovers, and many others. When the plumage is highly

protective or of dull uniform tints, as in many of the thrushes and

warblers, the sexes are almost or quite identical in colour; but when

any rich markings or bright tints are acquired, they are almost always

wanting or much fainter in the female, as we see in the black-cap among

warblers, and the chaffinch among finches.

It is in tropical regions, where from a variety of causes colour has

been, developed to its fullest extent, that we find the most remarkable

examples of sexual divergence of colour. The most gorgeously coloured

birds known are the birds of paradise, the chatterers, the tanagers, the

humming-birds, and the pheasant-tribe, including the peacocks. In all

these the females are much less brilliant, and, in the great majority of

cases, exceptionally plain and dull coloured birds. Not only are the

remarkable plumes, crests, and gorgets of the birds of paradise entirely

wanting in the females, but these latter are usually without any bright

colour at all, and rank no higher than our thrushes in ornamental

plumage. Of the humming-birds the same may be said, except that the

females are often green, and sometimes slightly metallic, but from their

small size and uniform tints are never conspicuous. The glorious blues

and purples, the pure whites and intense crimsons of the male chatterers

are represented in the females by olive-greens or dull browns, as are

the infinitely varied tints of the male tanagers. And in pheasants, the

splendour of plumage which characterises the males is entirely absent in

the females, which, though often ornamental, have always comparatively

sober and protective tints. The same thing occurs with many other

groups. In the Eastern tropics are many brilliant birds belonging to the

families of the warblers, flycatchers, shrikes, etc., but the female is

always much less brilliant than the male and often quite dull coloured.

\_Cause of Dull Colours of Female Birds.\_

The reason of this phenomenon is not difficult to find, if we consider

the essential conditions of a bird's existence, and the most important

function it has to fulfil. In order that the species may be continued,

young birds must be produced, and the female birds have to sit

assiduously on their eggs. While doing this they are exposed to

observation and attack by the numerous devourers of eggs and birds, and

it is of vital importance that they should be protectively coloured in

all those parts of the body which are exposed during incubation. To

secure this end all the bright colours and showy ornaments which

decorate the male have not been acquired by the female, who often

remains clothed in the sober hues which were probably once common to the

whole order to which she belongs. The different amounts of colour

acquired by the females have no doubt depended on peculiarities of

habits and of environment, and on the powers of defence or of

concealment possessed by the species. Mr. Darwin has taught us that

natural selection cannot produce absolute, but only relative perfection;

and as a protective colour is only one out of many means by which the

female birds are able to provide for the safety of their young, those

which are best endowed in other respects will have been allowed to

acquire more colour than those with whom the struggle for existence is

more severe.

\_Relation of Sex Colour to Nesting Habits.\_

This principle is strikingly illustrated by the existence of

considerable numbers of birds in which both sexes are similarly and

brilliantly coloured,--in some cases as brilliantly as the males of many

of the groups above referred to. Such are the extensive families of the

kingfishers, the woodpeckers, the toucans, the parrots, the turacos, the

hangnests, the starlings, and many other smaller groups, all the species

of which are conspicuously or brilliantly coloured, while in all of them

the females are either coloured exactly like the males, or, when

differently coloured, are equally conspicuous. When searching for some

cause for this singular apparent exception to the rule of female

protective colouring, I came upon a fact which beautifully explains it;

for in all these cases, without exception, the species either nests in

holes in the ground or in trees, or builds a domed or covered nest, so

as completely to conceal the sitting-bird. We have here a case exactly

parallel to that of the butterflies protected by distastefulness, whose

females are either exactly like the males, or, if different, are equally

conspicuous. We can hardly believe that so exact a parallel should exist

between such remote classes of animals, except under the influence of a

general law; and, in the need of protection by all defenceless animals,

and especially by most female insects and birds, we have such a law,

which has been proved to have influenced the colours of a considerable

proportion of the animal kingdom.[122]

The general relation which exists between the mode of nesting and the

coloration of the sexes in those groups of birds which need protection

from enemies, may be thus expressed: When both sexes are brilliant or

conspicuous, the nest is such as to conceal the sitting-bird; but when

the male is brightly coloured and the female sits exposed on the nest,

she is always less brilliant and generally of quite sober and protective

hues.

It must be understood that the mode of nesting has influenced the

colour, not that the colour has determined the mode of nesting; and

this, I believe, has been generally, though not perhaps universally, the

case. For we know that colour varies more rapidly, and can be more

easily modified and fixed by selection, than any other character;

whereas habits, especially when connected with structure, and when they

pervade a whole group, are much more persistent and more difficult to

change, as shown by the habit of the dog turning round two or three

times before lying down, believed to be that of the wild ancestral form

which thus smoothed down the herbage so as to form a comfortable bed. We

see, too, that the general mode of nesting is characteristic of whole

families differing widely in size, form, and colours. Thus, all the

kingfishers and their allies in every part of the world nest in holes,

usually in banks, but sometimes in trees. The motmots and the puff-birds

(Bucconidae) build in similar places; while the toucans, barbets,

trogons, woodpeckers, and parrots all make their nests in hollow trees.

This habit, pervading all the members of extensive families, must

therefore be extremely ancient, more especially as it evidently depends

in some degree on the structure of the birds, the bills, and especially

the feet, of all these groups being unfitted for the construction of

woven arboreal nests.[123] But in all these families the colour varies

greatly from species to species, being constant only in the one

character of the similarity of the sexes, or, at all events, in their

being equally conspicuous even though differently coloured.

When I first put forward this view of the connection between the mode of

nesting and the coloration of female birds, I expressed the law in

somewhat different terms, which gave rise to some misunderstanding, and

led to numerous criticisms and objections. Several cases were brought

forward in which the females were far less brilliant than the males,

although the nest was covered. This is the case with the Maluridae, or

superb warblers of Australia, in which the males are very brilliant

during the pairing season and the females quite plain, yet they build

domed nests. Here, there can be little doubt, the covered nest is a

protection from rain or from some special enemies to the eggs; while the

birds themselves are protectively coloured in both sexes, except for a

short time during the breeding season when the male acquires brilliant

colours; and this is probably connected with the fact of their

inhabiting the open plains and thin scrub of Australia, where protective

colours are as generally advantageous as they are in our north-temperate

zones.

As I have now stated the law, I do not think there are any exceptions to

it, while there are an overwhelming number of cases which give it a

strong support. It has been objected that the domed nests of many birds

are as conspicuous as the birds themselves would be, and would,

therefore, be of no use as a protection to the birds and young. But, as

a matter of fact, they do protect from attack, for hawks or crows do not

pluck such nests to pieces, as in doing so they would be exposed to the

attack of the whole colony; whereas a hawk or falcon could carry off a

sitting-bird or the young at a swoop, and entirely avoid attack.

Moreover, each kind of covered nest is doubtless directed against the

attacks of the most dangerous enemies of the species, the purse-like

nests, often a yard long, suspended from the extremity of thin twigs,

being useful against the attacks of snakes, which, if they attempted to

enter them, would be easily made to lose their hold and fall to the

ground. Such birds as jays, crows, magpies, hawks, and other birds of

prey, have also been urged as an exception; but these are all aggressive

birds, able to protect themselves, and thus do not need any special

protection for their females during nidification. Some birds which build

in covered nests are comparatively dull coloured, like many of the

weaver birds, but in others the colours are more showy, and in all the

sexes are alike; so that none of these are in any way opposed to the

rule. The golden orioles have, however, been adduced as a decided

exception, since the females are showy and build in an open nest. But

even here the females are less brilliant than the males, and are

sometimes greenish or olivaceous on the upper surface; while they very

carefully conceal their nests among dense foliage, and the male is

sufficiently watchful and pugnacious to drive off most intruders.

On the other hand, how remarkable it is that the only small and brightly

coloured birds of our own country in which the male and female are

alike--the tits and starlings--either build in holes or construct

covered nests; while the beautiful hangnests (Icteridae) of South

America, which always build covered or purse-shaped nests, are equally

showy in both sexes, in striking contrast with the chatterers and

tanagers of the same country, whose females are invariably less

conspicuous than the males. On a rough estimate, there are about 1200

species of birds in the class of showy males and females, with concealed

nidification; while there are probably, from an equally rough estimate,

about the same number in the contrasted class of showy males and dull

females, with open nests. This will leave the great bulk of known birds

in the classes of those which are more or less protectively coloured in

both sexes; or which, from their organisation and habits, do not

require special protective coloration, such as many of the birds of

prey, the larger waders, and the oceanic birds.

There are a few very curious cases in which the female bird is actually

more brilliant than the male, and which yet have open nests. Such are

the dotterel (Eudromias morinellus), several species of phalarope, an

Australian creeper (Climacteris erythropus), and a few others; but in

every one of these cases the relation of the sexes in regard to

nidification is reversed, the male performing the duties of incubation,

while the female is the stronger and more pugnacious. This curious case,

therefore, quite accords with the general law of coloration.[124]

\_Sexual Colours of other Vertebrates.\_

We may consider a few of the cases of sexual colouring of other classes

of vertebrates, as given by Mr. Darwin. In fishes, though the sexes are

usually alike, there are several species in which the males are more

brightly coloured, and have more elongated fins, spines, or other

appendages, and in some few cases the colours are decidedly different.

The males often fight together, and are altogether more vivacious and

excitable than the females during the breeding season; and with this we

may connect a greater intensity of coloration.

In frogs and toads the colours are usually alike, or a little more

intense in the males, and the same may be said of most snakes. It is in

lizards that we first meet with considerable sexual differences, many of

the species having gular pouches, frills, dorsal crests, or horns,

either confined to the males, or more developed in them than in the

females, and these ornaments are often brightly coloured. In most cases,

however, the tints of lizards are protective, the male being usually a

little more intense in coloration; and the difference in extreme cases

may be partly due to the need of protection for the female, which, when

laden with eggs, must be less active and less able to escape from

enemies than the male, and may, therefore, have retained more protective

colours, as so many insects and birds have certainly done.[125]

In mammalia there is often a somewhat greater intensity of colour in

the male, but rarely a decided difference. The female of the great red

kangaroo, however, is a delicate gray; while in the Lemur macaco of

Madagascar the male is jet-black and the female brown. In many monkeys

also there are some differences of colour, especially on the face. The

sexual weapons and ornaments of male mammalia, as horns, crests, manes,

and dewlaps, are well known, and are very numerous and remarkable.

Having thus briefly reviewed the facts, we will now consider the

theories to which they have given rise.

\_Sexual Selection by the Struggles of Males.\_

Among the higher animals it is a very general fact that the males fight

together for the possession of the females. This leads, in polygamous

animals especially, to the stronger or better armed males becoming the

parents of the next generation, which inherits the peculiarities of the

parents; and thus vigour and offensive weapons are continually increased

in the males, resulting in the strength and horns of the bull, the tusks

of the boar, the antlers of the stag, and the spurs and fighting

instinct of the gamecock. But almost all male animals fight together,

though not specially armed; even hares, moles, squirrels, and beavers

fight to the death, and are often found to be scarred and wounded. The

same rule applies to almost all male birds; and these battles have been

observed in such different groups as humming-birds, finches,

goatsuckers, woodpeckers, ducks, and waders. Among reptiles, battles of

the males are known to occur in the cases of crocodiles, lizards, and

tortoises; among fishes, in those of salmon and sticklebats. Even among

insects the same law prevails; and male spiders, beetles of many groups,

crickets, and butterflies often fight together.

From this very general phenomenon there necessarily results a form of

natural selection which increases the vigour and fighting power of the

male animal, since, in every case, the weaker are either killed,

wounded, or driven away. This selection would be more powerful if males

were always in excess of females, but after much research Mr. Darwin

could not obtain any satisfactory evidence that this was the case. The

same effect, however, is produced in some cases by constitution or

habits; thus male insects usually emerge first from the pupa, and among

migrating birds the males arrive first both in this country and in North

America. The struggle is thus intensified, and the most vigorous males

are the first to have offspring. This in all probability is a great

advantage, as the early breeders have the start in securing food, and

the young are strong enough to protect themselves while the later broods

are being produced.

It is to this form of male rivalry that Mr. Darwin first applied the

term "sexual selection." It is evidently a real power in nature; and to

it we must impute the development of the exceptional strength, size, and

activity of the male, together with the possession of special offensive

and defensive weapons, and of all other characters which arise from the

development of these or are correlated with them. But he has extended

the principle into a totally different field of action, which has none

of that character of constancy and of inevitable result that attaches to

natural selection, including male rivalry; for by far the larger portion

of the phenomena, which he endeavours to explain by the direct action of

sexual selection, can only be so explained on the hypothesis that the

immediate agency is female choice or preference. It is to this that he

imputes the origin of all secondary sexual characters other than weapons

of offence and defence, of all the ornamental crests and accessory

plumes of birds, the stridulating sounds of insects, the crests and

beards of monkeys and other mammals, and the brilliant colours and

patterns of male birds and butterflies. He even goes further, and

imputes to it a large portion of the brilliant colour that occurs in

both sexes, on the principle that variations occurring in one sex are

sometimes transmitted to the same sex only, sometimes to both, owing to

peculiarities in the laws of inheritance. In this extension of sexual

selection to include the action of female choice or preference, and in

the attempt to give to that choice such wide-reaching effects, I am

unable to follow him more than a very little way; and I will now state

some of the reasons why I think his views are unsound.

\_Sexual Characters due to Natural Selection.\_

Besides the acquisition of weapons by the male for the purpose of

fighting with other males, there are some other sexual characters which

may have been produced by natural selection. Such are the various sounds

and odours which are peculiar to the male, and which serve as a call to

the female or as an indication of his presence. These are evidently a

valuable addition to the means of recognition of the two sexes, and are

a further indication that the pairing season has arrived; and the

production, intensification, and differentiation of these sounds and

odours are clearly within the power of natural selection. The same

remark will apply to the peculiar calls of birds, and even to the

singing of the males. These may well have originated merely as a means

of recognition between the two sexes of a species, and as an invitation

from the male to the female bird. When the individuals of a species are

widely scattered, such a call must be of great importance in enabling

pairing to take place as early as possible, and thus the clearness,

loudness, and individuality of the song becomes a useful character, and

therefore the subject of natural selection. Such is especially the case

with the cuckoo, and with all solitary birds, and it may have been

equally important at some period of the development of all birds. The

act of singing is evidently a pleasurable one; and it probably serves as

an outlet for superabundant nervous energy and excitement, just as

dancing, singing, and field sports do with us. It is suggestive of this

view that the exercise of the vocal power seems to be complementary to

the development of accessory plumes and ornaments, all our finest

singing birds being plainly coloured, and with no crests, neck or tail

plumes to display; while the gorgeously ornamented birds of the tropics

have no song, and those which expend much energy in display of plumage,

as the turkey, peacocks, birds of paradise, and humming-birds, have

comparatively an insignificant development of voice. Some birds have, in

the wings or tail, peculiarly developed feathers which produce special

sounds. In some of the little manakins of Brazil, two or three of the

wing-feathers are curiously shaped and stiffened in the male, so that

the bird is able to produce with them a peculiar snapping or cracking

sound; and the tail-feathers of several species of snipe are so narrowed

as to produce distinct drumming, whistling, or switching sounds when the

birds descend rapidly from a great height. All these are probably

recognition and call notes, useful to each species in relation to the

most important function of their lives, and thus capable of being

developed by the agency of natural selection.

\_Decorative Plumage of Birds and its Display.\_

Mr. Darwin has devoted four chapters of his \_Descent of Man\_ to the

colours of birds, their decorative plumage, and its display at the

pairing season; and it is on this latter circumstance that he founds his

theory, that both the plumage and the colours have been developed by the

preference of the females, the more ornamented males becoming the

parents of each successive generation. Any one who reads these most

interesting chapters will admit, that the fact of the display is

demonstrated; and it may also be admitted, as highly probable, that the

female is pleased or excited by the display. But it by no means follows

that slight differences in the shape, pattern, or colours of the

ornamental plumes are what lead a female to give the preference to one

male over another; still less that all the females of a species, or the

great majority of them, over a wide area of country, and for many

successive generations, prefer exactly the same modification of the

colour or ornament.

The evidence on this matter is very scanty, and in most cases not at all

to the point. Some peahens preferred an old pied peacock; albino birds

in a state of nature have never been seen paired with other birds; a

Canada goose paired with a Bernicle gander; a male widgeon preferred a

pintail duck to its own species; a hen canary preferred a male

greenfinch to either linnet, goldfinch, siskin, or chaffinch. These

cases are evidently exceptional, and are not such as generally occur in

nature; and they only prove that the female does exert some choice

between very different males, and some observations on birds in a state

of nature prove the same thing; but there is no evidence that slight

variations in the colour or plumes, in the way of increased intensity or

complexity, are what determines the choice. On the other hand, Mr.

Darwin gives much evidence that it is \_not\_ so determined. He tells us

that Messrs. Hewitt, Tegetmeier, and Brent, three of the highest

authorities and best observers, "do not believe that the females prefer

certain males on account of the beauty of their plumage." Mr. Hewitt was

convinced "that the female almost invariably prefers the most vigorous,

defiant, and mettlesome male;" and Mr. Tegetmeier, "that a gamecock,

though disfigured by being dubbed, and with his hackles trimmed, would

be accepted as readily as a male retaining all his natural

ornaments."[126] Evidence is adduced that a female pigeon will sometimes

turn antipathy to a particular male without any assignable cause; or, in

other cases, will take a strong fancy to some one bird, and will desert

her own mate for him; but it is not stated that superiority or

inferiority of plumage has anything to do with these fancies. Two

instances are indeed given, of male birds being rejected, which had lost

their ornamental plumage; but in both cases (a widow-finch and a silver

pheasant) the long tail-plumes are the indication of sexual maturity.

Such cases do not support the idea that males with the tail-feathers a

trifle longer, or the colours a trifle brighter, are generally

preferred, and that those which are only a little inferior are as

generally rejected,--and this is what is absolutely needed to establish

the theory of the development of these plumes by means of the choice of

the female.

It will be seen, that female birds have unaccountable likes and dislikes

in the matter of their partners, just as we have ourselves, and this may

afford us an illustration. A young man, when courting, brushes or curls

his hair, and has his moustache, beard, or whiskers in perfect order,

and no doubt his sweetheart admires them; but this does not prove that

she marries him on account of these ornaments, still less that hair,

beard, whiskers, and moustache were developed by the continued

preferences of the female sex. So, a girl likes to see her lover well

and fashionably dressed, and he always dresses as well as he can when he

visits her; but we cannot conclude from this that the whole series of

male costumes, from the brilliantly coloured, puffed, and slashed

doublet and hose of the Elizabethan period, through the gorgeous coats,

long waistcoats, and pigtails of the early Georgian era, down to the

funereal dress-suit of the present day, are the direct result of female

preference. In like manner, female birds may be charmed or excited by

the fine display of plumage by the males; but there is no proof whatever

that slight differences in that display have any effect in determining

their choice of a partner.

\_Display of Decorative Plumage.\_

The extraordinary manner in which most birds display their plumage at

the time of courtship, apparently with the full knowledge that it is

beautiful, constitutes one of Mr. Darwin's strongest arguments. It is,

no doubt, a very curious and interesting phenomenon, and indicates a

connection between the exertion of particular muscles and the

development of colour and ornament; but, for the reasons just given, it

does not prove that the ornament has been developed by female choice.

During excitement, and when the organism develops superabundant energy,

many animals find it pleasurable to exercise their various muscles,

often in fantastic ways, as seen in the gambols of kittens, lambs, and

other young animals. But at the time of pairing, male birds are in a

state of the most perfect development, and possess an enormous store of

vitality; and under the excitement of the sexual passion they perform

strange antics or rapid flights, as much probably from an internal

impulse to motion and exertion as with any desire to please their mates.

Such are the rapid descent of the snipe, the soaring and singing of the

lark, and the dances of the cock-of-the-rock and of many other birds.

It is very suggestive that similar strange movements are performed by

many birds which have no ornamental plumage to display. Goatsuckers,

geese, carrion vultures, and many other birds of plain plumage have been

observed to dance, spread their wings or tails, and perform strange

love-antics. The courtship of the great albatross, a most unwieldy and

dull coloured bird, has been thus described by Professor Moseley: "The

male, standing by the female on the nest, raises his wings, spreads his

tail and elevates it, throws up his head with the bill in the air, or

stretches it straight out, or forwards, as far as he can, and then

utters a curious cry."[127] Mr. Jenner Weir informs me that "the male

blackbird is full of action, spreads out his glossy wing and tail, turns

his rich golden beak towards the female, and chuckles with delight,"

while he has never seen the more plain coloured thrush demonstrative to

the female. The linnet distends his rosy breast, and slightly expands

his brown wings and tail; while the various gay coloured Australian

finches adopt such attitudes and postures as, in every case, to show off

their variously coloured plumage to the best advantage.[128]

\_A Theory of Animal Coloration.\_

Having rejected Mr. Darwin's theory of female choice as incompetent to

account for the brilliant colours and markings of the higher animals,

the preponderance of these colours and markings in the male sex, and

their display during periods of activity or excitement, I may be asked

what explanation I have to offer as a preferable substitute. In my

\_Tropical Nature\_ I have already indicated such a theory, which I will

now briefly explain, supporting it by some additional facts and

arguments, which appear to me to have great weight, and for which I am

mainly indebted to a most interesting and suggestive posthumous work by

Mr. Alfred Tylor.[129]

The fundamental or ground colours of animals ar has been shown in

preceding chapters, very largely protective, and it is not improbable

that the primitive colours of all animals were so. During the long

course of animal development other modes of protection than concealment

by harmony of colour arose, and thenceforth the normal development of

colour due to the complex chemical and structural changes ever going on

in the organism, had full play; and the colours thus produced were again

and again modified by natural selection for purposes of warning,

recognition, mimicry, or special protection, as has been already fully

explained in the preceding chapters.

Mr. Taylor has, however, called attention to an important principle

which underlies the various patterns or ornamental markings of

animals--namely, that diversified coloration follows the chief lines of

structure, and changes at points, such as the joints, where function

changes. He says, "If we take highly decorated species--that is, animals

marked by alternate dark or light bands or spots, such as the zebra,

some deer, or the carnivora, we find, first, that the region of the

spinal column is marked by a dark stripe; secondly, that the regions of

the appendages, or limbs, are differently marked; thirdly, that the

flanks are striped or spotted, along or between the regions of the lines

of the ribs; fourthly, that the shoulder and hip regions are marked by

curved lines; fifthly, that the pattern changes, and the direction of

the lines, or spots, at the head, neck, and every joint of the limbs;

and lastly, that the tips of the ears, nose, tail, and feet, and the eye

are emphasised in colour. In spotted animals the greatest length of the

spot is generally in the direction of the largest development of the

skeleton."

This structural decoration is well seen in many insects. In

caterpillars, similar spots and markings are repeated in each segment,

except where modified for some form of protection. In butterflies, the

spots and bands usually have reference to the form of the wing and the

arrangement of the nervures; and there is much evidence to show that the

primitive markings are always spots in the cells, or between the

nervures, or at the junctions of nervures, the extension and coalescence

of these spots forming borders, bands, or blotches, which have become

modified in infinitely varied ways for protection, warning, or

recognition. Even in birds, the distribution of colours and markings

follows generally the same law. The crown of the head, the throat, the

ear-coverts, and the eyes have usually distinct tints in all highly

coloured birds; the region of the furcula has often a distinct patch of

colour, as have the pectoral muscles, the uropygium or root of the tail,

and the under tail-coverts.[130]

Mr. Tylor was of opinion the primitive form of ornamentation consisted

of spots, the confluence of these in certain directions forming lines or

bands; and, these again, sometimes coalescing into blotches, or into

more or less uniform tints covering a large portion of the surface of

the body. The young lion and tiger are both spotted; and in the Java hog

(Sus vittatus) very young animals are banded, but have spots over the

shoulders and thighs. These spots run into stripes as the animal grows

older; then the stripes expand, and at last, meeting together, the adult

animal becomes of a uniform dark brown colour. So many of the species of

deer are spotted when young, that Darwin concludes the ancestral form,

from which all deer are derived, must have been spotted. Pigs and tapirs

are banded or spotted when young; an imported young specimen of Tapirus

Bairdi was covered with white spots in longitudinal rows, here and there

forming short stripes.[131] Even the horse, which Darwin supposes to be

descended from a striped animal, is often spotted, as in dappled horses;

and great numbers show a tendency to spottiness, especially on the

haunches.

Ocelli may also be developed from spots, or from bars, as pointed out by

Mr. Darwin. Spots are an ordinary form of marking in disease, and these

spots sometimes run together, forming blotches. There is evidence that

colour markings are in some way dependent on nerve distribution. In the

disease known as frontal herpes, an eruption occurs which corresponds

exactly to the distribution of the ophthalmic division of the fifth

cranial nerve, mapping out all its little branches even to the one which

goes to the tip of the nose. In a Hindoo suffering from herpes the

pigment was destroyed in the arm along the course of the ulnar nerve,

with its branches along both sides of one finger and the half of

another. In the leg the sciatic and scaphenous nerves were partly mapped

out, giving to the patient the appearance of an anatomical diagram.[132]

These facts are very interesting, because they help to explain the

general dependence of marking on structure which has been already

pointed out. For, as the nerves everywhere follow the muscles, and these

are attached to the various bones, we see how it happens, that the

tracts in which distinct developments of colour appear, should so often

be marked out by the chief divisions of the bony structure in

vertebrates, and by the segments in the annulosa. There is, however,

another correspondence of even greater interest and importance.

Brilliant colours usually appear just in proportion to the development

of tegumentary appendages. Among birds the most brilliant colours are

possessed by those which have developed frills, crests, and elongated

tails like the humming-birds; immense tail-coverts like the peacock;

enormously expanded wing-feathers, as in the argus-pheasant; or

magnificent plumes from the region of the coracoids in many of the birds

of paradise. It is to be noted, also, that all these accessory plumes

spring from parts of the body which, in other species, are distinguished

by patches of colour; so that we may probably impute the development of

colour and of accessory plumage to the same fundamental cause.

Among insects, the most brilliant and varied coloration occurs in the

butterflies and moths, groups in which the wing-membranes have received

their greatest expansion, and whose specialisation has been carried

furthest in the marvellous scaly covering which is the seat of the

colour. It is suggestive, that the only other group in which functional

wings are much coloured is that of the dragonflies, where the membrane

is exceedingly expanded. In like manner, the colours of beetles, though

greatly inferior to those of the lepidoptera, occur in a group in which

the anterior pair of wings has been thickened and modified in order to

protect the vital parts, and in which these wing-covers (elytra), in the

course of development in the different groups, must have undergone great

changes, and have been the seat of very active growth.

\_The Origin of Accessory Plumes.\_

Mr. Darwin supposes, that these have in almost every case been developed

by the preference of female birds for such males as possessed them in a

higher degree than others; but this theory does not account for the fact

that these plumes usually appear in a few definite parts of the body. We

require some cause to initiate the development in one part rather than

in another. Now, the view that colour has arisen over surfaces where

muscular and nervous development is considerable, and the fact that it

appears especially upon the accessory or highly developed plumes, leads

us to inquire whether the same cause has not primarily determined the

development of these plumes. The immense tuft of golden plumage in the

best known birds of paradise (Paradisea apoda and P. minor) springs

from a very small area on the side of the breast. Mr. Frank E. Beddard,

who has kindly examined a specimen for me, says that "this area lies

upon the pectoral muscles, and near to the point where the fibres of the

muscle converge towards their attachment to the humerus. The plumes

arise, therefore, close to the most powerful muscle of the body, and

near to where the activities of that muscle would be at a maximum.

Furthermore, the area of attachment of the plumes is just above the

point where the arteries and nerves for the supply of the pectoral

muscles, and neighbouring regions, leave the interior of the body. The

area of attachment of the plume is, also, as you say in your letter,

just above the junction of the coracoid and sternum." Ornamental plumes

of considerable size rise from the same part in many other species of

paradise birds, sometimes extending laterally in front, so as to form

breast shields. They also occur in many humming-birds, and in some

sun-birds and honey-suckers; and in all these cases there is a wonderful

amount of activity and rapid movement, indicating a surplus of vitality,

which is able to manifest itself in the development of these accessory

plumes.[133]

In a quite distinct set of birds, the gallinaceae, we find the

ornamental plumage usually arising from very different parts, in the

form of elongated tail-feathers or tail-coverts, and of ruffs or hackles

from the neck. Here the wings are comparatively little used, the most

constant activities depending on the legs, since the gallinaceae are

pre-eminently walking, running, and scratching birds. Now the

magnificent train of the peacock--the grandest development of accessory

plumes in this order--springs from an oval or circular area, about three

inches in diameter, just above the base of the tail, and, therefore,

situated over the lower part of the spinal column near the insertion of

the powerful muscles which move the hind limbs and elevate the tail. The

very frequent presence of neck-ruffs or breast-shields in the males of

birds with accessory plumes may be partly due to selection, because they

must serve as a protection in their mutual combats, just as does the

lion's or the horse's mane. The enormously lengthened plumes of the bird

of paradise and of the peacock can, however, have no such use, but must

be rather injurious than beneficial in the bird's ordinary life. The

fact that they have been developed to so great an extent in a few

species is an indication of such perfect adaptation to the conditions of

existence, such complete success in the battle for life, that there is,

in the adult male at all events, a surplus of strength, vitality, and

growth-power which is able to expend itself in this way without injury.

That such is the case is shown by the great abundance of most of the

species which possess these wonderful superfluities of plumage. Birds of

paradise are among the commonest birds in New Guinea, and their loud

voices can be often heard when the birds themselves are invisible in the

depths of the forest; while Indian sportsmen have described the peafowl

as being so abundant, that from twelve to fifteen hundred have been seen

within an hour at one spot; and they range over the whole country from

the Himalayas to Ceylon. Why, in allied species, the development of

accessory plumes has taken different forms, we are unable to say, except

that it may be due to that individual variability which has served as

the starting-point for so much of what seems to us strange in form, or

fantastic in colour, both in the animal and vegetable world.

\_Development of Accessory Plumes and their Display.\_

If we have found a \_vera causa\_ for the origin of ornamental appendages

of birds and other animals in a surplus of vital energy, leading to

abnormal growths in those parts of the integument where muscular and

nervous action are greatest, the continuous development of these

appendages will result from the ordinary action of natural selection in

preserving the most healthy and vigorous individuals, and the still

further selective agency of sexual struggle in giving to the very

strongest and most energetic the parentage of the next generation. And,

as all the evidence goes to show that, so far as female birds exercise

any choice, it is of "the most vigorous, defiant, and mettlesome male,"

this form of sexual selection will act in the same direction, and help

to carry on the process of plume development to its culmination. That

culmination will be reached when the excessive length or abundance of

the plumes begins to be injurious to the bearer of them; and it may be

this check to the further lengthening of the peacock's train that has

led to the broadening of the feathers at the ends, and the consequent

production of the magnificent eye-spots which now form its crowning

ornament.

The display of these plumes will result from the same causes which led

to their production. Just in proportion as the feathers themselves

increased in length and abundance, the skin-muscles which serve to

elevate them would increase also; and the nervous development as well as

the supply of blood to these parts being at a maximum, the erection of

the plumes would become a habit at all periods of nervous or sexual

excitement. The display of the plumes, like the existence of the plumes

themselves, would be the chief external indication of the maturity and

vigour of the male, and would, therefore, be necessarily attractive to

the female. We have, thus, no reason for imputing to her any of those

aesthetic emotions which are excited in us, by the beauty of form,

colour, and pattern of these plumes; or the still more improbable

aesthetic tastes, which would cause her to choose her mate on account of

minute differences in their forms, colours, or patterns.

As co-operating causes in the production of accessory ornamental plumes,

I have elsewhere suggested[134] that crests and other erectile feathers

may have been useful in making the bird more formidable in appearance,

and thus serving to frighten away enemies; while long tail or wing

feathers might serve to distract the aim of a bird of prey. But though

this might be of some use in the earlier stages of their development, it

is probably of little importance compared with the vigour and pugnacity

of which the plumes are the indication, and which enable most of their

possessors to defend themselves against the enemies which are dangerous

to weaker and more timid birds. Even the tiny humming-birds are said to

attack birds of prey that approach too near to their nests.

\_The Effect of Female Preference will be Neutralised by Natural

Selection.\_

The various facts and arguments now briefly set forth, afford an

explanation of the phenomena of male ornament, as being due to the

general laws of growth and development, and make it unnecessary to call

to our aid so hypothetical a cause as the cumulative action of female

preference. There remains, however, a general argument, arising from the

action of natural selection itself, which renders it almost

inconceivable that female preference could have been effective in the

way suggested; while the same argument strongly supports the view here

set forth. Natural selection, as we have seen in our earlier chapters,

acts perpetually and on an enormous scale in weeding out the "unfit" at

every stage of existence, and preserving only those which are in all

respects the very best. Each year, only a small percentage of young

birds survive to take the place of the old birds which die; and the

survivors will be those which are best able to maintain existence from

the egg onwards, an important factor being that their parents should be

well able to feed and protect them, while they themselves must in turn

be equally able to feed and protect their own offspring. Now this

extremely rigid action of natural selection must render any attempt to

select mere ornament utterly nugatory, unless the most ornamented always

coincide with "the fittest" in every other respect; while, if they do so

coincide, then any selection of ornament is altogether superfluous. If

the most brightly coloured and fullest plumaged males are \_not\_ the most

healthy and vigorous, have \_not\_ the best instincts for the proper

construction and concealment of the nest, and for the care and

protection of the young, they are certainly not the fittest, and will

not survive, or be the parents of survivors. If, on the other hand,

there \_is\_ generally this correlation--if, as has been here argued,

ornament is the natural product and direct outcome of superabundant

health and vigour, then no other mode of selection is needed to account

for the presence of such ornament. The action of natural selection does

not indeed disprove the existence of female selection of ornament as

ornament, but it renders it entirely ineffective; and as the direct

evidence for any such female selection is almost \_nil\_, while the

objections to it are certainly weighty, there can be no longer any

reason for upholding a theory which was provisionally useful in calling

attention to a most curious and suggestive body of facts, but which is

now no longer tenable. The term "sexual selection" must, therefore, be

restricted to the direct results of male struggle and combat. This is

really a form of natural selection, and is a matter of direct

observation; while its results are as clearly deducible as those of any

of the other modes in which selection acts. And if this restriction of

the term is needful in the case of the higher animals it is much more so

with the lower. In butterflies the weeding out by natural selection

takes place to an enormous extent in the egg, larva, and pupa states;

and perhaps not more than one in a hundred of the eggs laid produces a

perfect insect which lives to breed. Here, then, the impotence of female

selection, if it exist, must be complete; for, unless the most

brilliantly coloured males are those which produce the best protected

eggs, larvae, and pupae, and unless the particular eggs, larvae, and

pupae, which are able to survive, are those which produce the most

brilliantly coloured butterflies, any choice the female might make must

be completely swamped. If, on the other hand, there \_is\_ this

correlation between colour development and perfect adaptation to

conditions in all stages, then this development will necessarily proceed

by the agency of natural selection and the general laws which determine

the production of colour and of ornamental appendages.[135]

\_General Laws of Animal Coloration.\_

The condensed account which has now been given of the phenomena of

colour in the animal world will sufficiently show the wonderful

complexity and extreme interest of the subject; while it affords an

admirable illustration of the importance of the great principle of

utility, and of the effect of the theories of natural selection and

development in giving a new interest to the most familiar facts of

nature. Much yet remains to be done, both in the observation of new

facts as to the relations between the colours of animals and their

habits or economy, and, more especially, in the elucidation of the laws

of growth which determine changes of colour in the various groups; but

so much is already known that we are able, with some confidence, to

formulate the general principles which have brought about all the beauty

and variety of colour which everywhere delight us in our contemplation

of animated nature. A brief statement of these principles will fitly

conclude our exposition of the subject.

1. Colour may be looked upon as a necessary result of the highly complex

chemical constitution of animal tissues and fluids. The blood, the bile,

the bones, the fat, and other tissues have characteristic, and often

brilliant colours, which we cannot suppose to have been determined for

any special purpose, as colours, since they are usually concealed. The

external organs, with their various appendages and integuments, would,

by the same general laws, naturally give rise to a greater variety of

colour.

2. We find it to be the fact that colour increases in variety and

intensity as external structures and dermal appendages become more

differentiated and developed. It is on scales, hair, and especially on

the more highly specialised feathers, that colour is most varied and

beautiful; while among insects colour is most fully developed in those

whose wing membranes are most expanded, and, as in the lepidoptera, are

clothed with highly specialised scales. Here, too, we find an additional

mode of colour production in transparent lamellae or in fine surface

striae which, by the laws of interference, produce the wonderful

metallic hues of so many birds and insects.

3. There are indications of a progressive change of colour, perhaps in

some definite order, accompanying the development of tissues or

appendages. Thus spots spread and fuse into bands, and when a lateral or

centrifugal expansion has occurred--as in the termination of the

peacocks' train feathers, the outer web of the secondary quills of the

Argus pheasant, or the broad and rounded wings of many butterflies--into

variously shaded or coloured ocelli. The fact that we find gradations of

colour in many of the more extensive groups, from comparatively dull or

simple to brilliant and varied hues, is an indication of some such law

of development, due probably to progressive local segregation in the

tissues of identical chemical or organic molecules, and dependent on

laws of growth yet to be investigated.

4. The colours thus produced, and subject to much individual variation,

have been modified in innumerable ways for the benefit of each species.

The most general modification has been in such directions as to favour

concealment when at rest in the usual surroundings of the species,

sometimes carried on by successive steps till it has resulted in the

most minute imitation of some inanimate object or exact mimicry of some

other animal. In other cases bright colours or striking contrasts have

been preserved, to serve as a warning of inedibility or of dangerous

powers of attack. Most frequent of all has been the specialisation of

each distinct form by some tint or marking for purposes of easy

recognition, especially in the case of gregarious animals whose safety

largely depends upon association and mutual defence.

5. As a general rule the colours of the two sexes are alike; but in the

higher animals there appears a tendency to deeper or more intense

colouring in the male, due probably to his greater vigour and

excitability. In many groups in which this superabundant vitality is at

a maximum, the development of dermal appendages and brilliant colours

has gone on increasing till it has resulted in a great diversity between

the sexes; and in most of these cases there is evidence to show that

natural selection has caused the female to retain the primitive and more

sober colours of the group for purposes of protection.

\_Concluding Remarks.\_

The general principles of colour development now sketched out enable us

to give some rational explanation of the wonderful amount of brilliant

colour which occurs among tropical animals. Looking on colour as a

normal product of organisation, which has either been allowed free play,

or has been checked and modified for the benefit of the species, we can

see at once that the luxuriant and perennial vegetation of the tropics,

by affording much more constant means of concealment, has rendered

brilliant colour less hurtful there than in the temperate and colder

regions. Again, this perennial vegetation supplies abundance of both

vegetable and insect food throughout the year, and thus a greater

abundance and greater variety of the forms of life are rendered

possible, than where recurrent seasons of cold and scarcity reduce the

possibilities of life to a minimum. Geology furnishes us with another

reason, in the fact, that throughout the tertiary period tropical

conditions prevailed far into the temperate regions, so that the

possibilities of colour development were still greater than they are at

the present time. The tropics, therefore, present to us the results of

animal development in a much larger area and under more favourable

conditions than prevail to-day. We see in them samples of the

productions of an earlier and a better world, from an animal point of

view; and this probably gives a greater variety and a finer display of

colour than would have been produced, had conditions always been what

they are now. The temperate zones, on the other hand, have recently

suffered the effects of a glacial period of extreme severity, with the

result that almost the only gay coloured birds they now possess are

summer visitors from tropical or sub-tropical lands. It is to the

unbroken and almost unchecked course of development from remote

geological times that has prevailed in the tropics, favoured by abundant

food and perennial shelter, that we owe such superb developments as the

frills and crests and jewelled shields of the humming-birds, the golden

plumes of the birds of paradise, and the resplendent train of the

peacock. This last exhibits to us the culmination of that marvel and

mystery of animal colour which is so well expressed by a poet-artist in

the following lines. The marvel will ever remain to the sympathetic

student of nature, but I venture to hope that in the preceding chapters

I have succeeded in lifting--if only by one of its corners--the veil of

mystery which has for long shrouded this department of nature.

\_On a Peacock's Feather.\_

In Nature's workshop but a shaving,

Of her poem but a word,

But a tint brushed from her palette,

This feather of a bird!

Yet set it in the sun glance,

Display it in the shine,

Take graver's lens, explore it,

Note filament and line,

Mark amethyst to sapphire,

And sapphire to gold,

And gold to emerald changing

The archetype unfold!

Tone, tint, thread, tissue, texture,

Through every atom scan,

Conforming still, developing,

Obedient to plan.

This but to form a pattern

On the garment of a bird!

What then must be the poem,

This but its lightest word!

Sit before it; ponder o'er it,

'Twill thy mind advantage more,

Than a treatise, than a sermon,

Than a library of lore.

FOOTNOTES:

[Footnote 118: Darwin's \_Descent of Man\_, p. 271.]

[Footnote 119: Darwin's \_Descent of Man\_, p. 294, and footnote.]

[Footnote 120: \_Nature\_, 1871, p. 489.]

[Footnote 121: Darwin in \_Nature\_, 1880, p. 237.]

[Footnote 122: See the author's \_Contributions to Natural Selection\_,

chap. vii. in which these facts were first brought forward.]

[Footnote 123: On this point see the author's \_Contributions to Natural

Selection\_, chap. v. i.]

[Footnote 124: Seebohm's \_History of British Birds\_, vol. ii.,

introduction, p. xiii.]

[Footnote 125: For details see Darwin's \_Descent of Man\_, chap. xii.]

[Footnote 126: \_Descent of Man\_, pp. 417, 418, 420.]

[Footnote 127: \_Notes of a Naturalist on the Challenger.\_]

[Footnote 128: \_Descent of Man\_, pp. 401, 402.]

[Footnote 129: \_Coloration in Animals and Plants\_, London, 1886.]

[Footnote 130: \_Coloration of Animals\_, Pl. X, p. 90; and Pls. II, III,

and IV, pp. 30, 40, 42.]

[Footnote 131: See coloured Fig. in \_Proc. Zool. Soc.\_, 1871, p. 626.]

[Footnote 132: A. Tylor's \_Coloration\_, p. 40; and Photograph in

Hutchinson's \_Illustrations of Clinical Surgery\_, quoted by Tylor.]

[Footnote 133: For activity and pugnacity of humming-birds, see

\_Tropical Nature\_, pp. 130, 213.]

[Footnote 134: \_Tropical Nature\_, p. 209. In Chapter V of this work the

views here advocated were first set forth, and the reader is referred

there for further details.]

[Footnote 135: The Rev. O. Pickard-Cambridge, who has devoted himself to

the study of spiders, has kindly sent me the following extract from a

letter, written in 1869, in which he states his views on this

question:--

"I myself doubt that particular application of the Darwinian

theory which attributes male peculiarities of form, structure,

colour, and ornament to female appetency or predilection. There

is, it seems to me, undoubtedly something in the male

organisation of a special, and sexual nature, which, of its own

vital force, develops the remarkable male peculiarities so

commonly seen, and of no imaginable use to that sex. In as far

as these peculiarities show a great vital power, they point out

to us the finest and strongest individuals of the sex, and show

us which of them would most certainly appropriate to themselves

the best and greatest number of females, and leave behind them

the strongest and greatest number of progeny. And here would

come in, as it appears to me, the proper application of Darwin's

theory of Natural Selection; for the possessors of greatest

vital power being those most frequently produced and reproduced,

the external signs of it would go on developing in an

ever-increasing exaggeration, only to be checked where it became

really detrimental in some respect or other to the individual."

This passage, giving the independent views of a close observer--one,

moreover, who has studied the species of an extensive group of animals

both in the field and in the laboratory--very nearly accords with my own

conclusions above given; and, so far as the matured opinions of a

competent naturalist have any weight, afford them an important support.]

CHAPTER XI

THE SPECIAL COLOURS OF PLANTS: THEIR ORIGIN AND PURPOSE

The general colour relations of plants--Colours of fruits--The

meaning of nuts--Edible or attractive fruits--The colours of

flowers--Modes of securing cross-fertilisation--The

interpretation of the facts--Summary of additional facts bearing

on insect fertilisation--Fertilisation of flowers by

birds--Self-fertilisation of flowers--Difficulties and

contradictions--Intercrossing not necessarily

advantageous--Supposed evil results of close interbreeding--How

the struggle for existence acts among flowers--Flowers the

product of insect agency--Concluding remarks on colour in

nature.

The colours of plants are both less definite and less complex than are

those of animals, and their interpretation on the principle of utility

is, on the whole, more direct and more easy. Yet here, too, we find that

in our investigation of the uses of the various colours of fruits and

flowers, we are introduced to some of the most obscure recesses of

nature's workshop, and are confronted with problems of the deepest

interest and of the utmost complexity.

So much has been written on this interesting subject since Mr. Darwin

first called attention to it, and its main facts have become so

generally known by means of lectures, articles, and popular books, that

I shall give here a mere outline sketch, for the purpose of leading up

to a discussion of some of the more fundamental problems which arise out

of the facts, and which have hitherto received less attention than they

deserve.

\_The General Colour Relations of Plants.\_

The green colour of the foliage of leafy plants is due to the existence

of a substance called chlorophyll, which is almost universally developed

in the leaves under the action of light. It is subject to definite

chemical changes during the processes of growth and of decay, and it is

owing to these changes that we have the delicate tints of spring

foliage, and the more varied, intense, and gorgeous hues of autumn. But

these all belong to the class of intrinsic or normal colours, due to the

chemical constitution of the organism; as colours they are unadaptive,

and appear to have no more relation to the wellbeing of the plants

themselves than have the colours of gems and minerals. We may also

include in the same category those algae and fungi which have bright

colours--the "red snow" of the arctic regions, the red, green, or purple

seaweeds, the brilliant scarlet, yellow, white, or black agarics, and

other fungi. All these colours are probably the direct results of

chemical composition or molecular structure, and, being thus normal

products of the vegetable organism, need no special explanation from our

present point of view; and the same remark will apply to the varied

tints of the bark of trunks, branches, and twigs, which are often of

various shades of brown and green, or even vivid reds or yellows.

There are, however, a few cases in which the need of protection, which

we have found to be so important an agency in modifying the colours of

animals, has also determined those of some of the smaller members of the

vegetable kingdom. Dr. Burchell found a mesembryanthomum in South Africa

like a curiously shaped pebble, closely resembling the stones among

which it grew;[136] and Mr. J.P. Mansel Weale states that in the same

country one of the Asclepiadeae has tubers growing above ground among

stones which they exactly resemble, and that, when not in leaf, they are

for this reason quite invisible.[137] It is clear that such resemblances

must be highly useful to these plants, inhabiting an arid country

abounding in herbivorous mammalia, which, in times of drought or

scarcity, will devour everything in the shape of a fleshy stem or tuber.

True mimicry is very rare in plants, though adaptation to like

conditions often produces in foliage and habit a similarity that is

deceiving. Euphorbias growing in deserts often closely resemble cacti.

Seaside plants and high alpine plants of different orders are often much

alike; and innumerable resemblances of this kind are recorded in the

names of plants, as Veronica epacridea (the veronica like an epacris),

Limnanthemum nymphaeoides (the limnanthemum like a nymphaea), the

resembling species in each case belonging to totally distinct families.

But in these cases, and in most others that have been observed, the

essential features of true mimicry are absent, inasmuch as the one plant

cannot be supposed to derive any benefit from its close resemblance to

the other, and this is still more certain from the fact that the two

species usually inhabit different localities. A few cases exist,

however, in which there does seem to be the necessary accordance and

utility. Mr. Mansel Weale mentions a labiate plant (Ajuga ophrydis), the

only species of the genus Ajuga in South Africa, which is strikingly

like an orchid of the same country; while a balsam (Impatiens capensis),

also a solitary species of the genus in that country, is equally like an

orchid, growing in the same locality and visited by the same insects. As

both these genera of plants are specialised for insect fertilisation,

and both of the plants in question are isolated species of their

respective genera, we may suppose that, when they first reached South

Africa they were neglected by the insects of the country; but, being

both remotely like orchids in form of flower, those varieties that

approached nearest to the familiar species of the country were visited

by insects and cross-fertilised, and thus a closer resemblance would at

length be brought about. Another case of close general resemblance, is

that of our common white dead-nettle (Lamium album) to the

stinging-nettle (Urtica dioica); and Sir John Lubbock thinks that this

is a case of true mimicry, the dead-nettle being benefited by being

mistaken by grazing animals for the stinging-nettle.[138]

\_Colours of Fruits.\_

It is when we come to the essential parts of plants on which their

perpetuation and distribution depends, that we find colour largely

utilised for a distinct purpose in flowers and fruits. In the former we

find attractive colours and guiding marks to secure cross-fertilisation

by insects; in the latter attractive or protective coloration, the first

to attract birds or other animals when the fruits are intended to be

eaten, the second to enable them to escape being eaten when it would be

injurious to the species. The colour phenomena of fruits being much the

most simple will be considered first.

The perpetuation and therefore the very existence of each species of

flowering plant depend upon its seeds being preserved from destruction

and more or less effectually dispersed over a considerable area. The

dispersal is effected either mechanically or by the agency of animals.

Mechanical dispersal is chiefly by means of air-currents, and large

numbers of seeds are specially adapted to be so carried, either by being

clothed with down or pappus, as in the well-known thistle and dandelion

seeds; by having wings or other appendages, as in the sycamore, birch,

and many other trees; by being thrown to a considerable distance by the

splitting of the seed-vessel, and by many other curious devices.[139]

Very large numbers of seeds, however, are so small and light that they

can be carried enormous distances by gales of wind, more especially as

most of this kind are flattened or curved, so as to expose a large

surface in proportion to their weight. Those which are carried by

animals have their surfaces, or that of the seed-vessel, armed with

minute hooks, or some prickly covering which attaches itself to the hair

of mammalia or the feathers of birds, as in the burdock, cleavers, and

many other species. Others again are sticky, as in Plumbago europaea,

mistletoe, and many foreign plants.

All the seeds or seed-vessels which are adapted to be dispersed in any

of these ways are of dull protective tints, so that when they fall on

the ground they are almost indistinguishable; besides which, they are

usually small, hard, and altogether unattractive, never having any

soft, juicy pulp; while the edible seeds often bear such a small

proportion to the hard, dry envelopes or appendages, that few animals

would care to eat them.

\_The Meaning of Nuts.\_

There is, however, another class of fruits or seeds, usually termed

nuts, in which there is a large amount of edible matter, often very

agreeable to the taste, and especially attractive and nourishing to a

large number of animals. But when eaten, the seed is destroyed and the

existence of the species endangered. It is evident, therefore, that it

is by a kind of accident that these nuts are eatable; and that they are

not intended to be eaten is shown by the special care nature seems to

have taken to conceal or to protect them. We see that all our common

nuts are green when on the tree, so as not easily to be distinguished

from the leaves; but when ripe they turn brown, so that when they fall

on to the ground they are equally indistinguishable among the dead

leaves and twigs, or on the brown earth. Then they are almost always

protected by hard coverings, as in hazel-nuts, which are concealed by

the enlarged leafy involucre, and in the large tropical brazil-nuts and

cocoa-nuts by such a hard and tough case as to be safe from almost every

animal. Others have an external bitter rind, as in the walnut; while in

the chestnuts and beech-nuts two or three fruits are enclosed in a

prickly involucre.

Notwithstanding all these precautions, nuts are largely devoured by

mammalia and birds; but as they are chiefly the product of trees or

shrubs of considerable longevity, and are generally produced in great

profusion, the perpetuation of the species is not endangered. In some

cases the devourers of nuts may aid in their dispersal, as they probably

now and then swallow the seed whole, or not sufficiently crushed to

prevent germination; while squirrels have been observed to bury nuts,

many of which are forgotten and afterwards grow in places they could not

have otherwise reached.[140] Nuts, especially the larger kinds which are

so well protected by their hard, nearly globular cases, have their

dispersal facilitated by rolling down hill, and more especially by

floating in rivers and lakes, and thus reaching other localities. During

the elevation of land areas this method would be very effective, as the

new land would always be at a lower level than that already covered with

vegetation, and therefore in the best position for being stocked with

plants from it.

The other modes of dispersal of seeds are so clearly adapted to their

special wants, that we feel sure they must have been acquired by the

process of variation and natural selection. The hooked and sticky seeds

are always those of such herbaceous plants as are likely, from their

size, to come in contact with the wool of sheep or the hair of cattle;

while seeds of this kind never occur on forest trees, on aquatic plants,

or even on very dwarf creepers or trailers. The winged seed-vessels or

seeds, on the other hand, mostly belong to trees and to tall shrubs or

climbers. We have, therefore, a very exact adaptation to conditions in

these different modes of dispersal; while, when we come to consider

individual cases, we find innumerable other adaptations, some of which

the reader will find described in the little work by Sir John Lubbock

already referred to.

\_Edible or Attractive Fruits.\_

It is, however, when we come to true fruits (in a popular sense) that we

find varied colours evidently intended to attract animals, in order that

the fruits may be eaten, while the seeds pass through the body

undigested and are then in the fittest state for germination. This end

has been gained in a great variety of ways, and with so many

corresponding adaptations as to leave no doubt as to the value of the

result. Fruits are pulpy or juicy, and usually sweet, and form the

favourite food of innumerable birds and some mammals. They are always

coloured so as to contrast with the foliage or surroundings, red being

the most common as it is certainly the most conspicuous colour, but

yellow, purple, black, or white being not uncommon. The edible portion

of fruits is developed from different parts of the floral envelopes, or

of the ovary, in the various orders and genera. Sometimes the calyx

becomes enlarged and fleshy, as in the apple and pear tribe; more often

the integuments of the ovary itself are enlarged, as in the plum, peach,

grape, etc.; the receptacle is enlarged and forms the fruit of the

strawberry; while the mulberry, pineapple, and fig are examples of

compound fruits formed in various ways from a dense mass of flowers.

In all cases the seeds themselves are protected from injury by various

devices. They are small and hard in the strawberry, raspberry, currant,

etc., and are readily swallowed among the copious pulp. In the grape

they are hard and bitter; in the rose (hip) disagreeably hairy; in the

orange tribe very bitter; and all these have a smooth, glutinous

exterior which facilitates their being swallowed. When the seeds are

larger and are eatable, they are enclosed in an excessively hard and

thick covering, as in the various kinds of "stone" fruit (plums,

peaches, etc.), or in a very tough core, as in the apple. In the nutmeg

of the Eastern Archipelago we have a curious adaptation to a single

group of birds. The fruit is yellow, somewhat like an oval peach, but

firm and hardly eatable. This splits open and shows the glossy black

covering of the seed or nutmeg, over which spreads the bright scarlet

arillus or "mace," an adventitious growth of no use to the plant except

to attract attention. Large fruit pigeons pluck out this seed and

swallow it entire for the sake of the mace, while the large nutmeg

passes through their bodies and germinates; and this has led to the wide

distribution of wild nutmegs over New Guinea and the surrounding

islands.

In the restriction of bright colour to those edible fruits the eating of

which is beneficial to the plant, we see the undoubted result of natural

selection; and this is the more evident when we find that the colour

never appears till the fruit is ripe--that is, till the seeds within it

are fully matured and in the best state for germination. Some

brilliantly coloured fruits are poisonous, as in our bitter-sweet

(Solanum dulcamara), cuckoo-pint (Arum) and the West Indian manchineel.

Many of these are, no doubt, eaten by animals to whom they are harmless;

and it has been suggested that even if some animals are poisoned by them

the plant is benefited, since it not only gets dispersed, but finds, in

the decaying body of its victim, a rich manure heap.[141] The particular

colours of fruits are not, so far as we know, of any use to them other

than as regards conspicuousness, hence a tendency to \_any\_ decided

colour has been preserved and accumulated as serving to render the fruit

easily visible among its surroundings of leaves or herbage. Out of 134

fruit-bearing plants in Mongredien's \_Trees and Shrubs\_, and Hooker's

\_British Flora\_, the fruits of no less than sixty-eight, or rather more

than half, are red, forty-five are black, fourteen yellow, and seven

white. The great prevalence of red fruits is almost certainly due to

their greater conspicuousness having favoured their dispersal, though it

may also have arisen in part from the chemical changes of chlorophyll

during ripening and decay producing red tints as in many fading leaves.

Yet the comparative scarcity of yellow in fruits, while it is the most

common tint of fading leaves, is against this supposition.

There are, however, a few instances of coloured fruits which do not seem

to be intended to be eaten; such are the colocynth plant (Cucumis

colocynthus), which has a beautiful fruit the size and colour of an

orange, but nauseous beyond description to the taste. It has a hard

rind, and may perhaps be dispersed by being blown along the ground, the

colour being an adventitious product; but it is quite possible,

notwithstanding its repulsiveness to us, that it may be eaten by some

animals. With regard to the fruit of another plant, Calotropis procera,

there is less doubt, as it is dry and full of thin, flat-winged seeds,

with fine silky filaments, eminently adapted for wind-dispersal; yet it

is of a bright yellow colour, as large as an apple, and therefore very

conspicuous. Here, therefore, we seem to have colour which is a mere

byproduct of the organism and of no use to it; but such cases are

exceedingly rare, and this rarity, when compared with the great

abundance of cases in which there is an obvious purpose in the colour,

adds weight to the evidence in favour of the theory of the attractive

coloration of edible fruits in order that birds and other animals may

assist in their dispersal. Both the above-named plants are natives of

Palestine and the adjacent arid countries.[142]

\_The Colours of Flowers.\_

Flowers are much more varied in their colours than fruits, as they are

more complex and more varied in form and structure; yet there is some

parallelism between them in both respects. Flowers are frequently

adapted to attract insects as fruits are to attract birds, the object

being in the former to secure cross-fertilisation, in the latter

dispersal; while just as colour is an index of the edibility of fruits

which supply pulp or juice to birds, so are the colours of flowers an

indication of the presence of nectar or of pollen which are devoured by

insects.

The main facts and many of the details, as to the relation of insects to

flowers, were discovered by Sprengel in 1793. He noticed the curious

adaptation of the structure of many flowers to the particular insects

which visit them; he proved that insects do cross-fertilise flowers, and

he believed that this was the object of the adaptations, while the

presence of nectar and pollen ensured the continuance of their visits;

yet he missed discovering the \_use\_ of this cross-fertilisation. Several

writers at a later period obtained evidence that cross-fertilisation of

plants was a benefit to them; but the wide generality of this fact and

its intimate connection with the numerous and curious adaptations

discovered by Sprengel, was first shown by Mr. Darwin, and has since

been demonstrated by a vast mass of observations, foremost among which

are his own researches on orchids, primulas, and other plants.[143]

By an elaborate series of experiments carried on for many years Mr.

Darwin demonstrated the great value of cross-fertilisation in increasing

the rapidity of growth, the strength and vigour of the plant, and in

adding to its fertility. This effect is produced immediately, not as he

expected would be the case, after several generations of crosses. He

planted seeds from cross-fertilised and self-fertilised plants on two

sides of the same pot exposed to exactly similar conditions, and in most

cases the difference in size and vigour was amazing, while the plants

from cross-fertilised parents also produced more and finer seeds. These

experiments entirely confirmed the experience of breeders of animals

already referred to (p. 160), and led him to enunciate his famous

aphorism, "Nature abhors perpetual self-fertilisation".[144] In this

principle we appear to have a sufficient reason for the various

contrivances by which so many flowers secure cross-fertilisation, either

constantly or occasionally. These contrivances are so numerous, so

varied, and often so highly complex and extraordinary, that they have

formed the subject of many elaborate treatises, and have also been amply

popularised in lectures and handbooks. It will be unnecessary,

therefore, to give details here, but the main facts will be summarised

in order to call attention to some difficulties of the theory which seem

to require further elucidation.

\_Modes of securing Cross-Fertilisation.\_

When we examine the various modes in which the cross-fertilisation of

flowers is brought about, we find that some are comparatively simple in

their operation and needful adjustments, others highly complex. The

simple methods belong to four principal classes:--(1) By dichogamy--that

is, by the anthers and the stigma becoming mature or in a fit state for

fertilisation at slightly different times on the same plant. The result

of this is that, as plants in different stations, on different soils, or

exposed to different aspects flower earlier or later, the mature pollen

of one plant can only fertilise some plant exposed to somewhat different

conditions or of different constitution, whose stigma will be mature at

the same time; and this difference has been shown by Darwin to be that

which is adapted to secure the fullest benefit of cross-fertilisation.

This occurs in Geranium pratense, Thymus serpyllum, Arum maculatum, and

many others. (2) By the flower being self-sterile with its own pollen,

as in the crimson flax. This absolutely prevents self-fertilisation. (3)

By the stamens and anthers being so placed that the pollen cannot fall

upon the stigma, while it does fall upon a visiting insect which carries

it to the stigma of another flower. This effect is produced in a variety

of very simple ways, and is often aided by the motion of the stamens

which bend down out of the way of the stigmas before the pollen is ripe,

as in Malva sylvestris (see Fig. 28). (4) By the male and female flowers

being on different plants, forming the class Dioecia of Linnaeus. In

these cases the pollen may be carried to the stigmas either by the wind

or by the agency of insects.

[Illustration: FIG. 28.

Malva sylvestris, adapted for insect-fertilisation.

Malva rotundifolia, adapted for self-fertilisation.]

Now these four methods are all apparently very simple, and easily

produced by variation and selection. They are applicable to flowers of

any shape, requiring only such size and colour as to attract insects,

and some secretion of nectar to ensure their repeated visits, characters

common to the great majority of flowers. All these methods are common,

except perhaps the second; but there are many flowers in which the

pollen from another plant is prepotent over the pollen from

fertilisation, the same flower, and this has nearly the same effect as

self-sterility if the flowers are frequently crossed by insects. We

cannot help asking, therefore, why have other and much more elaborate

methods been needed? And how have the more complex arrangements of so

many flowers been brought about? Before attempting to answer these

questions, and in order that the reader may appreciate the difficulty of

the problem and the nature of the facts to be explained, it will be

necessary to give a summary of the more elaborate modes of securing

cross-fertilisation.

(1) We first have dimorphism and heteromorphism, the phenomena of which

have been already sketched in our seventh chapter.

Here we have both a mechanical and a physiological modification, the

stamens and pistil being variously modified in length and position,

while the different stamens in the same flower have widely different

degrees of fertility when applied to the same stigma,--a phenomenon

which, if it were not so well established, would have appeared in the

highest degree improbable. The most remarkable case is that of the three

different forms of the loosestrife (Lythrum salicaria) here figured

(Fig. 29 on next page).

(2) Some flowers have irritable stamens which, when their bases are

touched by an insect, spring up and dust it with pollen. This occurs in

our common berberry.

[Illustration: FIG. 29.--Lythrum salicaria (Purple loosestrife).]

(3) In others there are levers or processes by which the anthers are

mechanically brought down on to the head or back of an insect entering

the flower, in such a position as to be carried to the stigma of the

next flower it visits. This may be well seen in many species of Salvia

and Erica.

(4) In some there is a sticky secretion which, getting on to the

proboscis of an insect, carries away the pollen, and applies it to the

stigma of another flower. This occurs in our common milkwort (Polygala

vulgaris).

(5) In papilionaceous plants there are many complex adjustments, such as

the squeezing out of pollen from a receptacle on to an insect, as in

Lotus corniculatus, or the sudden springing out and exploding of the

anthers so as thoroughly to dust the insect, as in Medicago falcata,

this occurring after the stigma has touched the insect and taken off

some pollen from the last flower.

(6) Some flowers or spathes form closed boxes in which insects find

themselves entrapped, and when they have fertilised the flower, the

fringe of hairs opens and allows them to escape. This occurs in many

species of Arum and Aristolochia.

(7) Still more remarkable are the traps in the flower of Asclepias which

catch flies, butterflies, and wasps by the legs, and the wonderfully

complex arrangements of the orchids. One of these, our common Orchis

pyramidalis, may be briefly described to show how varied and beautiful

are the arrangements to secure cross-fertilisation. The broad trifid lip

of the flower offers a support to the moth which is attracted by its

sweet odour, and two ridges at the base guide the proboscis with

certainty to the narrow entrance of the nectary. When the proboscis has

reached the end of the spur, its basal portion depresses the little

hinged rostellum that covers the saddle-shaped sticky glands to which

the pollen masses (pollinia) are attached. On the proboscis being

withdrawn, the two pollinia stand erect and parallel, firmly attached to

the proboscis. In this position, however, they would be useless, as they

would miss the stigmatic surface of the next flower visited by the moth.

But as soon as the proboscis is withdrawn, the two pollen masses begin

to diverge till they are exactly as far apart as are the stigmas of the

flower; and then commences a second movement which brings them down

till they project straight forward nearly at right angles to their first

position, so as exactly to hit against the stigmatic surfaces of the

next flower visited on which they leave a portion of their pollen. The

whole of these motions take about half a minute, and in that time the

moth will usually have flown to another plant, and thus effect the most

beneficial kind of cross-fertilisation.[145] This description will be

better understood by referring to the illustration opposite, from

Darwin's \_Fertilisation of Orchids\_(Fig. 30).

[Illustration: FIG. 30.--Orchis pyramidalis.]

\_The Interpretation of these Facts.\_

Having thus briefly indicated the general character of the more complex

adaptations for cross-fertilisation, the details of which are to be

found in any of the numerous works on the subject,[146] we find

ourselves confronted with the very puzzling question--Why were these

innumerable highly complex adaptations produced, when the very same

result may be effected--and often is effected--by extremely simple

means? Supposing, as we must do, that all flowers were once of simple

and regular forms, like a buttercup or a rose, how did such irregular

and often complicated flowers as the papilionaceous or pea family, the

labiates or sage family, and the infinitely varied and fantastic orchids

ever come into existence? No cause has yet been suggested but the need

of attracting insects to cross-fertilise them; yet the attractiveness of

regular flowers with bright colours and an ample supply of nectar is

equally great, and cross-fertilisation can be quite as effectively

secured in these by any of the four simple methods already described.

Before attempting to suggest a possible solution of this difficult

problem, we have yet to pass in review a large body of curious

adaptations connected with insect fertilisation, and will first call

attention to that portion of the phenomena which throw some light upon

the special colours of flowers in their relation to the various kinds of

insects which visit them. For these facts we are largely indebted to

the exact and long-continued researches of Professor Hermann MÃ¼ller.

\_Summary of Additional Facts bearing on Insect Fertilisation.\_

1. That the size and colour of a flower are important factors in

determining the visits of insects, is shown by the general fact of more

insects visiting conspicuous than inconspicuous flowers. As a single

instance, the handsome Geranium palustre was observed by Professor

MÃ¼ller to be visited by sixteen different species of insects, the

equally showy G. pratense by thirteen species, while the smaller and

much less conspicuous G. molle was visited by eight species, and G.

pusillum by only one. In many cases, however, a flower may be very

attractive to only a few species of insects; and Professor MÃ¼ller

states, as the result of many years' assiduous observation, that "a

species of flower is the more visited by insects the more conspicuous it

is."

2. Sweet odour is usually supplementary to the attraction of colour.

Thus it is rarely present in the largest and most gaudily coloured

flowers which inhabit open places, such as poppies, paeonies,

sunflowers, and many others; while it is often the accompaniment of

inconspicuous flowers, as the mignonette; of such as grow in shady

places, as the violet and primrose; and especially of white or yellowish

flowers, as the white jasmine, clematis, stephanotis, etc.

3. White flowers are often fertilised by moths, and very frequently give

out their scent only by night, as in our butterfly-orchis (Habenaria

chlorantha); and they sometimes open only at night, as do many of the

evening primroses and other flowers. These flowers are often long tubed

in accordance with the length of the moths' probosces, as in the genus

Pancratium, our butterfly orchis, white jasmine, and a host of others.

4. Bright red flowers are very attractive to butterflies, and are

sometimes specially adapted to be fertilised by them, as in many pinks

(Dianthus deltoides, D. superbus, D. atrorubens), the corn-cockle

(Lychnis Githago), and many others. Blue flowers are especially

attractive to bees and other hymenoptera (though they frequent flowers

of all colours), no less than sixty-seven species of this order having

been observed to visit the common "sheep's-bit" (Jasione montana). Dull

yellow or brownish flowers, some of which smell like carrion, are

attractive to flies, as the Arum and Aristolochia; while the dull

purplish flowers of the Scrophularia are specially attractive to wasps.

5. Some flowers have neither scent nor nectar, and yet attract insects

by sham nectaries! In the herb-paris (Paris quadrifolia) the ovary

glistens as if moist, and flies alight on it and carry away pollen to

another flower; while in grass of parnassus (Parnassia palustris) there

are a number of small stalked yellow balls near the base of the flower,

which look like drops of honey but are really dry. In this case there is

a little nectar lower down, but the special attraction is a sham; and as

there are fresh broods of insects every year, it takes time for them to

learn by experience, and thus enough are always deceived to effect

cross-fertilisation.[147] This is analogous to the case of the young

birds, which have to learn by experience the insects that are inedible,

as explained at page 253.

6. Many flowers change their colour as soon as fertilised; and this is

beneficial, as it enables bees to avoid wasting time in visiting those

blossoms which have been already fertilised and their nectar exhausted.

The common lungwort (Pulmonaria officinalis), is at first red, but later

turns blue; and H. MÃ¼ller observed bees visiting many red flowers in

succession, but neglecting the blue. In South Brazil there is a species

of Lantana, whose flowers are yellow the first day, orange the second,

and purple the third; and Dr. Fritz MÃ¼ller observed that many

butterflies visited the yellow flowers only, some both the yellow and

the orange flowers, but none the purple.

7. Many flowers have markings which serve as guides to insects; in some

cases a bright central eye, as in the borage and forget-me-not; or lines

or spots converging to the centre, as in geraniums, pinks, and many

others. This enables insects to go quickly and directly to the opening

of the flower, and is equally important in aiding them to obtain a

better supply of food, and to fertilise a larger number of flowers.

8. Flowers have been specially adapted to the kinds of insects that

most abound where they grow. Thus the gentians of the lowlands are

adapted to bees, those of the high alps to butterflies only; and while

most species of Rhinanthus (a genus to which our common "yellow rattle"

belongs) are bee-flowers, one high alpine species (R. alpinus) has been

also adapted for fertilisation by butterflies only. The reason of this

is, that in the high alps butterflies are immensely more plentiful than

bees, and flowers adapted to be fertilised by bees can often have their

nectar extracted by butterflies without effecting cross-fertilisation.

It is, therefore, important to have a modification of structure which

shall make butterflies the fertilisers, and this in many cases has been

done.[148]

9. Economy of time is very important both to the insects and the

flowers, because the fine working days are comparatively few, and if no

time is wasted the bees will get more honey, and in doing so will

fertilise more flowers. Now, it has been ascertained by several

observers that many insects, bees especially, keep to one kind of flower

at a time, visiting hundreds of blossoms in succession, and passing over

other species that may be mixed with them. They thus acquire quickness

in going at once to the nectar, and the change of colour in the flower,

or incipient withering when fertilised, enables them to avoid those

flowers that have already had their honey exhausted. It is probably to

assist the insects in keeping to one flower at a time, which is of vital

importance to the perpetuation of the species, that the flowers which

bloom intermingled at the same season are usually very distinct both in

form and colour. In the sandy districts of Surrey, in the early spring,

the copses are gay with three flowers--the primrose, the wood-anemone,

and the lesser celandine, forming a beautiful contrast, while at the

same time the purple and the white dead-nettles abound on hedge banks. A

little later, in the same copses, we have the blue wild hyacinth (Scilla

nutans), the red campion (Lychnis dioica), the pure white great starwort

(Stellaria Holosteum), and the yellow dead-nettle (Lamium Galeobdolon),

all distinct and well-contrasted flowers. In damp meadows in summer we

have the ragged robin (Lychnis Floscuculi), the spotted orchis (O.

maculata), and the yellow rattle (Rhinanthus Crista-galli); while in

drier meadows we have cowslips, ox-eye daisies, and buttercups, all very

distinct both in form and colour. So in cornfields we have the scarlet

poppies, the purple corn-cockle, the yellow corn-marygold, and the blue

cornflower; while on our moors the purple heath and the dwarf gorse make

a gorgeous contrast. Thus the difference of colour which enables the

insect to visit with rapidity and unerring aim a number of flowers of

the same kind in succession, serves to adorn our meadows, banks, woods,

and heaths with a charming variety of floral colour and form at each

season of the year.[149]

\_Fertilisation of Flowers by Birds.\_

In the temperate regions of the Northern Hemisphere, insects are the

chief agents in cross-fertilisation when this is not effected by the

wind; but in warmer regions, and in the Southern hemisphere, birds are

found to take a considerable part in the operation, and have in many

cases led to modifications in the form and colour of flowers. Each part

of the globe has special groups of birds which are flower-haunters.

America has the humming-birds (Trochilidae), and the smaller group of

the sugar-birds (Caerebidae). In the Eastern tropics the sun-birds

(Nectarineidae) take the place of the humming-birds, and another small

group, the flower-peckers (Dicaeidae), assist them. In the Australian

region there are also two flower-feeding groups, the Meliphagidae, or

honey-suckers, and the brush-tongued lories (Trichoglossidae). Recent

researches by American naturalists have shown that many flowers are

fertilised by humming-birds, such as passion-flowers, trumpet-flowers,

fuchsias, and lobelias; while some, as the Salvia splendens of Mexico,

are specially adapted to their visits. We may thus perhaps explain the

number of very large tubular flowers in the tropics, such as the huge

brugmansias and bignonias; while in the Andes and in Chile, where

humming-birds are especially plentiful, we find great numbers of red

tubular flowers, often of large size and apparently adapted to these

little creatures. Such are the beautiful Lapageria and Philesia, the

grand Pitcairneas, and the genera Fuchsia, Mitraria, Embothrium,

Escallonia, Desfontainea, Eccremocarpus, and many Gesneraceae. Among the

most extraordinary modifications of flower structure adapted to bird

fertilisation are the species of Marcgravia, in which the pedicels and

bracts of the terminal portion of a pendent bunch of flowers have been

modified into pitchers which secrete nectar and attract insects, while

birds feeding on the nectar, or insects, have the pollen of the

overhanging flowers dusted on their backs, and, carrying it to other

flowers, thus cross-fertilise them (see Illustration).

[Illustration: FIG. 31.--Humming-bird fertilising Marcgravia

nepenthoides.]

In Australia and New Zealand the fine "glory peas" (Clianthus), the

Sophora, Loranthus, many Epacrideae and Myrtaceae, and the large flowers

of the New Zealand flax (Phormium tenax), are cross-fertilised by

birds; while in Natal the fine trumpet-creeper (Tecoma capensis) is

fertilised by Nectarineas.

The great extent to which insect and bird agency is necessary to flowers

is well shown by the case of New Zealand. The entire country is

comparatively poor in species of insects, especially in bees and

butterflies which are the chief flower fertilisers; yet according to the

researches of local botanists no less than one-fourth of all the

flowering plants are incapable of self-fertilisation, and, therefore,

wholly dependent on insect or bird agency for the continuance of the

species.

The facts as to the cross-fertilisation of flowers which have now been

very briefly summarised, taken in connection with Darwin's experiments

proving the increased vigour and fertility given by cross-fertilisation,

seem amply to justify his aphorism that "Nature abhors

self-fertilisation," and his more precise statement, that, "No plant is

perpetually self-fertilised;" and this view has been upheld by

Hildebrand, Delpino, and other botanists.[150]

\_Self-Fertilisation of Flowers.\_

But all this time we have been only looking at one side of the question,

for there exists an abundance of facts which seem to imply, just as

surely, the utter uselessness of cross-fertilisation. Let us, then, see

what these facts are before proceeding further.

1. An immense variety of plants are habitually self-fertilised, and

their numbers probably far exceed those which are habitually

cross-fertilised by insects. Almost all the very small or obscure

flowered plants with hermaphrodite flowers are of this kind. Most of

these, however, may be insect fertilised occasionally, and may,

therefore, come under the rule that no species are perpetually

self-fertilised.

2. There are many plants, however, in which special arrangements exist

to secure self-fertilisation. Sometimes the corolla closes and brings

the anthers and stigma into contact; in others the anthers cluster round

the stigmas, both maturing together, as in many buttercups, stitchwort

(Stellaria media), sandwort (Spergula), and some willow-herbs

(Epilobium); or they arch over the pistil, as in Galium aparine and

Alisma Plantago. The style is also modified to bring it into contact

with the anthers, as in the dandelion, groundsel, and many other

plants.[151] All these, however, may be occasionally cross-fertilised.

3. In other cases precautions are taken to prevent cross-fertilisation,

as in the numerous cleistogamous or closed flowers. These occur in no

less than fifty-five different genera, belonging to twenty-four natural

orders, and in thirty-two of these genera the normal flowers are

irregular, and have therefore been specially modified for insect

fertilisation.[152] These flowers appear to be degradations of the

normal flowers, and are closed up by various modifications of the petals

or other parts, so that it is impossible for insects to reach the

interior, yet they produce seed in abundance, and are often the chief

means by which the species is continued. Thus, in our common dog-violet

the perfect flowers rarely produce seed, while the rudimentary

cleistogamic flowers do so in abundance. The sweet violet also produces

abundance of seed from its cleistogamic flowers, and few from its

perfect flowers; but in Liguria it produces only perfect flowers which

seed abundantly. No case appears to be known of a plant which has

cleistogamic flowers only, but a small rush (Juncus bufonius) is in this

condition in some parts of Russia, while in other parts perfect flowers

are also produced.[153] Our common henbit dead-nettle (Lamium

amplexicaule) produces cleistogamic flowers, as do also some orchids.

The advantage gained by the plant is great economy of specialised

material, since with very small flowers and very little expenditure of

pollen an abundance of seed is produced.

4. A considerable number of plants which have evidently been specially

modified for insect fertilisation have, by further modification, become

quite self-fertile. This is the case with the garden-pea, and also with

our beautiful bee-orchis, in which the pollen-masses constantly fall on

to the stigmas, and the flower, being thus self-fertilised, produces

abundance of capsules and of seed. Yet in many of its close allies

insect agency is absolutely required; but in one of these, the

fly-orchis, comparatively very little seed is produced, and

self-fertilisation would therefore be advantageous to it. When

garden-peas were artificially cross-fertilised by Mr. Darwin, it seemed

to do them no good, as the seeds from these crosses produced less

vigorous plants than seed from those which were self-fertilised; a fact

directly opposed to what usually occurs in cross-fertilised plants.

5. As opposed to the theory that there is any absolute need for

cross-fertilisation, it has been urged by Mr. Henslow and others that

many self-fertilised plants are exceptionally vigorous, such as

groundsel, chickweed, sow-thistle, buttercups, and other common weeds;

while most plants of world-wide distribution are self-fertilised, and

these have proved themselves to be best fitted to survive in the battle

of life. More than fifty species of common British plants are very

widely distributed, and all are habitually self-fertilised.[154] That

self-fertilisation has some great advantage is shown by the fact that it

is usually the species which have the smallest and least conspicuous

flowers which have spread widely, while the large and showy flowered

species of the same genera or families, which require insects to

cross-fertilise them, have a much more limited distribution.

6. It is now believed by some botanists that many inconspicuous and

imperfect flowers, including those that are wind-fertilised, such as

plantains, nettles, sedges, and grasses, do not represent primitive or

undeveloped forms, but are degradations from more perfect flowers which

were once adapted to insect fertilisation. In almost every order we find

some plants which have become thus reduced or degraded for wind or

self-fertilisation, as Poterium and Sanguisorba among the Rosaceae;

while this has certainly been the case in the cleistogamic flowers. In

most of the above-mentioned plants there are distinct rudiments of

petals or other floral organs, and as the chief use of these is to

attract insects, they could hardly have existed in primitive

flowers.[155] We know, moreover, that when the petals cease to be

required for the attraction of insects, they rapidly diminish in size,

lose their bright colour or almost wholly disappear.[156]

\_Difficulties and Contradictions.\_

The very bare summary that has now been given of the main facts relating

to the fertilisation of flowers, will have served to show the vast

extent and complexity of the inquiry, and the extraordinary

contradictions and difficulties which it presents. We have direct proof

of the beneficial results of intercrossing in a great number of cases;

we have an overwhelming mass of facts as to the varied and complex

structure of flowers evidently adapted to secure this intercrossing by

insect agency; yet we see many of the most vigorous plants which spread

widely over the globe, with none of these adaptations, and evidently

depending on self-fertilisation for their continued existence and

success in the battle of life. Yet more extraordinary is it to find

numerous cases in which the special arrangements for cross-fertilisation

appear to have been a failure, since they have either been supplemented

by special means for self-fertilisation, or have reverted back in

various degrees to simpler forms in which self-fertilisation becomes the

rule. There is also a further difficulty in the highly complex modes by

which cross-fertilisation is often brought about; for we have seen that

there are several very effective yet very simple modes of securing

intercrossing, involving a minimum of change in the form and structure

of the flower; and when we consider that the result attained with so

much cost of structural modification is by no means an unmixed good, and

is far less certain in securing the perpetuation of the species than is

self-fertilisation, it is most puzzling to find such complex methods

resorted to, sometimes to the extent of special precautions against the

possibility of self-fertilisation ever taking place. Let us now see

whether any light can be thrown on these various anomalies and

contradictions.

\_Intercrossing not necessarily Advantageous.\_

No one was more fully impressed than Mr. Darwin with the beneficial

effects of intercrossing on the vigour and fertility of the species or

race, yet he clearly saw that it was not always and necessarily

advantageous. He says: "The most important conclusion at which I have

arrived is, that the mere act of intercrossing by itself does no good.

The good depends on the individuals which are crossed differing slightly

in constitution, owing to their progenitors having been subjected during

several generations to slightly different conditions. This conclusion,

as we shall hereafter see, is closely connected with various important

physiological problems, such as the benefit derived from slight changes

in the conditions of life."[157] Mr. Darwin has also adduced much direct

evidence proving that slight changes in the conditions of life are

beneficial to both animals and plants, maintaining or restoring their

vigour and fertility in the same way as a favourable cross seems to

restore it.[158] It is, I believe, by a careful consideration of these

two classes of facts that we shall find the clue to the labyrinth in

which this subject has appeared to involve us.

\_Supposed Evil Results of Close Interbreeding.\_

Just as we have seen that intercrossing is not necessarily good, we

shall be forced to admit that close interbreeding is not necessarily

bad. Our finest breeds of domestic animals have been thus produced, and

by a careful statistical inquiry Mr. George Darwin has shown that the

most constant and long-continued intermarriages among the British

aristocracy have produced no prejudicial results. The rabbits on Porto

Santo are all the produce of a single female; they have lived on the

same small island for 470 years, and they still abound there and appear

to be vigorous and healthy (see p. 161).

We have, however, on the other hand, overwhelming evidence that in many

cases, among our domestic animals and cultivated plants, close

interbreeding does produce bad results, and the apparent contradiction

may perhaps be explained on the same general principles, and under

similar limitations, as were found to be necessary in defining the value

of intercrossing. It appears probable, then, that it is not

interbreeding in itself that is hurtful, but interbreeding without

rigid selection or some change of conditions. Under nature, as in the

case of the Porto Santo rabbits, the rapid increase of these animals

would in a very few years stock the island with a full population, and

thereafter natural selection would act powerfully in the preservation

only of the healthiest and the most fertile, and under these conditions

no deterioration would occur. Among the aristocracy there has been a

constant selection of beauty, which is generally synonymous with health,

while any constitutional infertility has led to the extinction of the

family. With domestic animals the selection practised is usually neither

severe enough nor of the right kind. There is no natural struggle for

existence, but certain points of form and colour characteristic of the

breed are considered essential, and thus the most vigorous or the most

fertile are not always those which are selected to continue the stock.

In nature, too, the species always extends over a larger area and

consists of much greater numbers, and thus a difference of constitution

soon arises in different parts of the area, which is wanting in the

limited numbers of pure bred domestic animals. From a consideration of

these varied facts we conclude that an occasional disturbance of the

organic equilibrium is what is essential to keep up the vigour and

fertility of any organism, and that this disturbance may be equally well

produced either by a cross between individuals of somewhat different

constitutions, or by occasional slight changes in the conditions of

life. Now plants which have great powers of dispersal enjoy a constant

change of conditions, and can, therefore, exist permanently, or at all

events, for very long periods, without intercrossing; while those which

have limited powers of dispersal, and are restricted to a comparatively

small and uniform area, need an occasional cross to keep up their

fertility and general vigour. We should, therefore, expect that those

groups of plants which are adapted both for cross-and

self-fertilisation, which have showy flowers and possess great powers of

seed-dispersal, would be the most abundant and most widely distributed;

and this we find to be the case, the Compositae possessing all these

characteristics in the highest degree, and being the most generally

abundant group of plants with conspicuous flowers in all parts of the

world.

\_How the Struggle for Existence Acts among Flowers.\_

Let us now consider what will be the action of the struggle for

existence under the conditions we have seen to exist.

Everywhere and at all times some species of plants will be dominant and

aggressive; while others will be diminishing in numbers, reduced to

occupy a smaller area, and generally having a hard struggle to maintain

themselves. Whenever a self-fertilising plant is thus reduced in numbers

it will be in danger of extinction, because, being limited to a small

area, it will suffer from the effects of too uniform conditions which

will produce weakness and infertility. But while this change is in

progress, any crosses between individuals of slightly different

constitution will be beneficial, and all variations favouring either

insect agency on the one hand, or wind-dispersal of pollen on the other,

will lead to the production of a somewhat stronger and more fertile

stock. Increased size or greater brilliancy of the flower, more abundant

nectar, sweeter odour, or adaptations for more effectual

cross-fertilisation would all be preserved, and thus would be initiated

some form of specialisation for insect agency in cross-fertilisation;

and in every different species so circumstanced the result would be

different, depending as it would on many and complex combinations of

variation of parts of the flower, and of the insect species which most

abounded in the district.

Species thus favourably modified might begin a new era of development,

and, while spreading over a somewhat wider area, give rise to new

varieties or species, all adapted in various degrees and modes to secure

cross-fertilisation by insect agency. But in course of ages some change

of conditions might prove adverse. Either the insects required might

diminish in numbers or be attracted by other competing flowers, or a

change of climate might give the advantage to other more vigorous

plants. Then self-fertilisation with greater means of dispersal might be

more advantageous; the flowers might become smaller and more numerous;

the seeds smaller and lighter so as to be more easily dispersed by the

wind, while some of the special adaptations for insect fertilisation

being useless would, by the absence of selection and by the law of

economy of growth, be reduced to a rudimentary form. With these

modifications the species might extend its range into new districts,

thereby obtaining increased vigour by the change of conditions, as

appears to have been the case with so many of the small flowered

self-fertilised plants. Thus it might continue to exist for a long

series of ages, till under other changes--geographical or biological--it

might again suffer from competition or from other adverse circumstances,

and be at length again confined to a limited area, or reduced to very

scanty numbers.

But when this cycle of change had taken place, the species would be very

different from the original form. The flower would have been at one time

modified to favour the visits of insects and to secure

cross-fertilisation by their aid, and when the need for this passed

away, some portions of these structures would remain, though in a

reduced or rudimentary condition. But when insect agency became of

importance a second time, the new modifications would start from a

different or more advanced basis, and thus a more complex result might

be produced. Owing to the unequal rates at which the reduction of the

various parts might occur, some amount of irregularity in the flower

might arise, and on a second development towards insect

cross-fertilisation this irregularity, if useful, might be increased by

variation and selection.

The rapidity and comparative certainty with which such changes as are

here supposed do really take place, are well shown by the great

differences in floral structure, as regards the mode of fertilisation,

in allied genera and species, and even in some cases in varieties of the

same species. Thus in the Ranunculaceae we find the conspicuous part of

the flower to be the petals in Ranunculus, the sepals in Helleborus,

Anemone, etc., and the stamens in most species of Thalictrum. In all

these we have a simple regular flower, but in Aquilegia it is made

complex by the spurred petals, and in Delphinium and Aconitum it becomes

quite irregular. In the more simple class self-fertilisation occurs

freely, but it is prevented in the more complex flowers by the stamens

maturing before the pistil. In the Caprifoliaceae we have small and

regular greenish flowers, as in the moschatel (Adoxa); more conspicuous

regular open flowers without honey, as in the elder (Sambucus); and

tubular flowers increasing in length and irregularity, till in some,

like our common honeysuckle, they are adapted for fertilisation by moths

only, with abundant honey and delicious perfume to attract them. In the

Scrophulariaceae we find open, almost regular flowers, as Veronica and

Verbascum, fertilised by flies and bees, but also self-fertilised;

Scrophularia adapted in form and colour to be fertilised by wasps; and

the more complex and irregular flowers of Linaria, Rhinanthus,

Melampyrum, Pedicularis, etc., mostly adapted to be fertilised by bees.

In the genera Geranium, Polygonum, Veronica, and several others there is

a gradation of forms from large and bright to small and obscure coloured

flowers, and in every case the former are adapted for insect

fertilisation, often exclusively, while in the latter self-fertilisation

constantly occurs. In the yellow rattle (Rhinanthus Crista-galli) there

are two forms (which have been named \_major\_ and \_minor\_), the larger

and more conspicuous adapted to insect fertilisation only, the smaller

capable of self-fertilisation; and two similar forms exist in the

eyebright (Euphrasia officinalis). In both these cases there are special

modifications in the length and curvature of the style as well as in the

size and shape of the corolla; and the two forms are evidently becoming

each adapted to special conditions, since in some districts the one, in

other districts the other is most abundant.[159]

These examples show us that the kind of change suggested above is

actually going on, and has presumably always been going on in nature

throughout the long geological epochs during which the development of

flowers has been progressing. The two great modes of gaining increased

vigour and fertility--intercrossing and dispersal over wider areas--have

been resorted to again and again, under the pressure of a constant

struggle for existence and the need for adaptation to ever-changing

conditions. During all the modifications that ensued, useless parts were

reduced or suppressed, owing to the absence of selection and the

principle of economy of growth; and thus at each fresh adaptation some

rudiments of old structures were re-developed, but not unfrequently in

a different form and for a distinct purpose.

The chief types of flowering plants have existed during the millions of

ages of the whole tertiary period, and during this enormous lapse of

time many of them may have been modified in the direction of insect

fertilisation, and again into that of self-fertilisation, not once or

twice only, but perhaps scores or even hundreds of times; and at each

such modification a difference in the environment may have led to a

distinct line of development. At one epoch the highest specialisation of

structure in adaptation to a single species or group of insects may have

saved a plant from extinction; while, at other times, the simplest mode

of self-fertilisation, combined with greater powers of dispersal and a

constitution capable of supporting diverse physical conditions, may have

led to a similar result. With some groups the tendency seems to have

been almost continuously to greater and greater specialisation, while

with others a tendency to simplification and degradation has resulted in

such plants as the grasses and sedges.

We are now enabled dimly to perceive how the curious anomaly of very

simple and very complex methods of securing cross-fertilisation--both

equally effective--may have been brought about. The simple modes may be

the result of a comparatively direct modification from the more

primitive types of flowers, which were occasionally, and, as it were,

accidentally visited and fertilised by insects; while the more complex

modes, existing for the most part in the highly irregular flowers, may

result from those cases in which adaptation to insect-fertilisation, and

partial or complete degradation to self-fertilisation or to

wind-fertilisation, have again and again recurred, each time producing

some additional complexity, arising from the working up of old rudiments

for new purposes, till there have been reached the marvellous flower

structures of the papilionaceous tribes, of the asclepiads, or of the

orchids.

We thus see that the existing diversity of colour and of structure in

flowers is probably the ultimate result of the ever-recurring struggle

for existence, combined with the ever-changing relations between the

vegetable and animal kingdoms during countless ages. The constant

variability of every part and organ, with the enormous powers of

increase possessed by plants, have enabled them to become again and

again readjusted to each change of condition as it occurred, resulting

in that endless variety, that marvellous complexity, and that exquisite

colouring which excite our admiration in the realm of flowers, and

constitute them the perennial charm and crowning glory of nature.

\_Flowers the Product of Insect Agency.\_

In his \_Origin of Species\_, Mr. Darwin first stated that flowers had

been rendered conspicuous and beautiful in order to attract insects,

adding: "Hence we may conclude that, if insects had not been developed

on the earth, our plants would not have been decked with beautiful

flowers, but would have produced only such poor flowers as we see on our

fir, oak, nut, and ash trees, on grasses, docks, and nettles, which are

all fertilised through the agency of the wind." The argument in favour

of this view is now much stronger than when he wrote; for not only have

we reason to believe that most of these wind-fertilised flowers are

degraded forms of flowers which have once been insect fertilised, but we

have abundant evidence that whenever insect agency becomes comparatively

ineffective, the colours of the flowers become less bright, their size

and beauty diminish, till they are reduced to such small, greenish,

inconspicuous flowers as those of the rupture-wort (Herniaria glabra),

the knotgrass (Polygonum aviculare), or the cleistogamic flowers of the

violet. There is good reason to believe, therefore, not only that

flowers have been developed in order to attract insects to aid in their

fertilisation, but that, having been once produced, in however great

profusion, if the insect races were all to become extinct, flowers (in

the temperate zones at all events) would soon dwindle away, and that

ultimately all floral beauty would vanish from the earth.

We cannot, therefore, deny the vast change which insects have produced

upon the earth's surface, and which has been thus forcibly and

beautifully delineated by Mr. Grant Allen: "While man has only tilled a

few level plains, a few great river valleys, a few peninsular mountain

slopes, leaving the vast mass of earth untouched by his hand, the insect

has spread himself over every land in a thousand shapes, and has made

the whole flowering creation subservient to his daily wants. His

buttercup, his dandelion, and his meadow-sweet grow thick in every

English field. His thyme clothes the hillside; his heather purples the

bleak gray moorland. High up among the alpine heights his gentian

spreads its lakes of blue; amid the snows of the Himalayas his

rhododendrons gleam with crimson light. Even the wayside pond yields him

the white crowfoot and the arrowhead, while the broad expanses of

Brazilian streams are beautified by his gorgeous water-lilies. The

insect has thus turned the whole surface of the earth into a boundless

flower-garden, which supplies him from year to year with pollen or

honey, and itself in turn gains perpetuation by the baits that it offers

for his allurement."[160]

\_Concluding Remarks on Colour in Nature.\_

In the last four chapters I have endeavoured to give a general and

systematic, though necessarily condensed view of the part which is

played by colour in the organic world. We have seen in what infinitely

varied ways the need of concealment has led to the modification of

animal colours, whether among polar snows or sandy deserts, in tropical

forests or in the abysses of the ocean. We next find these general

adaptations giving way to more specialised types of coloration, by which

each species has become more and more harmonised with its immediate

surroundings, till we reach the most curiously minute resemblances to

natural objects in the leaf and stick insects, and those which are so

like flowers or moss or birds' droppings that they deceive the acutest

eye. We have learnt, further, that these varied forms of protective

colouring are far more numerous than has been usually suspected,

because, what appear to be very conspicuous colours or markings when the

species is observed in a museum or in a menagerie, are often highly

protective when the creature is seen under the natural conditions of its

existence. From these varied classes of facts it seems not improbable

that fully one-half of the species in the animal kingdom possess colours

which have been more or less adapted to secure for them concealment or

protection.

Passing onward we find the explanation of a distinct type of colour or

marking, often superimposed upon protective tints, in the importance of

easy recognition by many animals of their fellows, their parents, or

their mates. By this need we have been able to account for markings that

seem calculated to make the animal conspicuous, when the general tints

and well-known habits of the whole group demonstrate the need of

concealment. Thus also we are able to explain the constant symmetry in

the markings of wild animals, as well as the numerous cases in which the

conspicuous colours are concealed when at rest and only become visible

during rapid motion. In striking contrast to ordinary protective

coloration we have "warning colours," usually very conspicuous and often

brilliant or gaudy, which serve to indicate that their possessors are

either dangerous or uneatable to the usual enemies of their tribe. This

kind of coloration is probably more prevalent than has been hitherto

supposed, because in the case of many tropical animals we are quite

unacquainted with their special and most dangerous enemies, and are also

unable to determine whether they are or are not distasteful to those

enemies. As a kind of corollary to the "warning colours," we find the

extraordinary phenomena of "mimicry," in which defenceless species

obtain protection by being mistaken for those which, from any cause,

possess immunity from attack. Although a large number of instances of

warning colour and of mimicry are now recorded, it is probably still an

almost unworked field of research, more especially in tropical regions

and among the inhabitants of the ocean.

The phenomena of sexual diversities of coloration next engaged our

attention, and the reasons why Mr. Darwin's theory of "sexual

selection," as regards colour and ornament, could not be accepted were

stated at some length, together with the theory of animal coloration and

ornament we propose to substitute for it. This theory is held to be in

harmony with the general facts of animal coloration, while it entirely

dispenses with the very hypothetical and inadequate agency of female

choice in producing the detailed colours, patterns, and ornaments, which

in so many cases distinguish the male sex.

If my arguments on this point are sound, they will dispose also of Mr.

Grant Allen's view of the direct action of the colour sense on the

animal integuments.[161] He argues that the colours of insects and birds

reproduce generally the colours of the flowers they frequent or the

fruits they eat, and he adduces numerous cases in which flower-haunting

insects and fruit-eating birds are gaily coloured. This he supposes to

be due to the colour-taste, developed by the constant presence of bright

flowers and fruits, being applied to the selection of each variation

towards brilliancy in their mates; thus in time producing the gorgeous

and varied hues they now possess. Mr. Allen maintains that "insects are

bright where bright flowers exist in numbers, and dull where flowers are

rare or inconspicuous;" and he urges that "we can hardly explain this

wide coincidence otherwise than by supposing that a taste for colour is

produced through the constant search for food among entomophilous

blossoms, and that this taste has reacted upon its possessors through

the action of unconscious sexual selection."

The examples Mr. Allen quotes of bright insects being associated with

bright flowers seem very forcible, but are really deceptive or

erroneous; and quite as many cases could be quoted which prove the very

opposite. For example, in the dense equatorial forests flowers are

exceedingly scarce, and there is no comparison with the amount of floral

colour to be met with in our temperate meadows, woods, and hillsides.

The forests about Para in the lower Amazon are typical in this respect,

yet they abound with the most gorgeously coloured butterflies, almost

all of which frequent the forest depths, keeping near the ground, where

there is the greatest deficiency of brilliant flowers. In contrast with

this let us take the Cape of Good Hope--the most flowery region probably

that exists upon the globe,--where the country is a complete

flower-garden of heaths, pelargoniums, mesembryanthemus, exquisite

iridaceous and other bulbs, and numerous flowering shrubs and trees; yet

the Cape butterflies are hardly equal, either in number or variety, to

those of any country in South Europe, and are utterly insignificant when

compared with those of the comparatively flowerless forest-depths of the

Amazon or of New Guinea. Neither is there any relation between the

colours of other insects and their haunts. Few are more gorgeous than

some of the tiger-beetles and the carabi, yet these are all carnivorous;

while many of the most brilliant metallic buprestidae and longicorns are

always found on the bark of fallen trees. So with the humming-birds;

their brilliant metallic tints can only be compared with metals or gems,

and are totally unlike the delicate pinks and purples, yellows and reds

of the majority of flowers. Again, the Australian honey-suckers

(Meliphagidae) are genuine flower-haunters, and the Australian flora is

more brilliant in colour display than that of most tropical regions, yet

these birds are, as a rule, of dull colours, not superior on the average

to our grain-eating finches. Then, again, we have the grand pheasant

family, including the gold and the silver pheasants, the gorgeous

fire-backed and ocellated pheasants, and the resplendent peacock, all

feeding on the ground on grain or seeds or insects, yet adorned with the

most gorgeous colours.

There is, therefore, no adequate basis of facts for this theory to rest

upon, even if there were the slightest reason to believe that not only

birds, but butterflies and beetles, take any delight in colour for its

own sake, apart from the food-supply of which it indicates the presence.

All that has been proved or that appears to be probable is, that they

are able to perceive differences of colour, and to associate each colour

with the particular flowers or fruits which best satisfy their wants.

Colour being in its nature diverse, it has been beneficial for them to

be able to distinguish all its chief varieties, as manifested more

particularly in the vegetable kingdom, and among the different species

of their own group; and the fact that certain species of insects show

some preference for a particular colour may be explained by their having

found flowers of that colour to yield them a more abundant supply of

nectar or of pollen. In those cases in which butterflies frequent

flowers of their own colour, the habit may well have been acquired from

the protection it affords them.

It appears to me that, in imputing to insects and birds the same love of

colour for its own sake and the same aesthetic tastes as we ourselves

possess, we may be as far from the truth as were those writers who held

that the bee was a good mathematician, and that the honeycomb was

constructed throughout to satisfy its refined mathematical instincts;

whereas it is now generally admitted to be the result of the simple

principle of economy of material applied to a primitive cylindrical

cell.[162]

In studying the phenomena of colour in the organic world we have been

led to realise the wonderful complexity of the adaptations which bring

each species into harmonious relation with all those which surround it,

and which thus link together the whole of nature in a network of

relations of marvellous intricacy. Yet all this is but, as it were, the

outward show and garment of nature, behind which lies the inner

structure--the framework, the vessels, the cells, the circulating

fluids, and the digestive and reproductive processes,--and behind these

again those mysterious chemical, electrical, and vital forces which

constitute what we term Life. These forces appear to be fundamentally

the same for all organisms, as is the material of which all are

constructed; and we thus find behind the outer diversities an inner

relationship which binds together the myriad forms of life.

Each species of animal or plant thus forms part of one harmonious whole,

carrying in all the details of its complex structure the record of the

long story of organic development; and it was with a truly inspired

insight that our great philosophical poet apostrophised the humble

weed--

Flower in the crannied wall,

I pluck you out of the crannies,

I hold you here, root and all, in my hand,

Little flower--but \_if\_ I could understand

What you are, root and all, and all in all,

I should know what God and man is.

FOOTNOTES:

[Footnote 136: Burchell's \_Travels\_, vol. i. p. 10.]

[Footnote 137: \_Nature\_, vol. iii. p. 507.]

[Footnote 138: \_Flowers, Fruits, and Leaves\_, p. 128 (Fig. 79).]

[Footnote 139: For a popular sketch of these, see Sir J. Lubbock's

\_Flowers, Fruits, and Leaves\_, or any general botanical work.]

[Footnote 140: \_Nature\_, vol. xv. p, 117.]

[Footnote 141: Grant Allen's \_Colour Sense\_, p. 113.]

[Footnote 142: Canon Tristram's \_Natural History of the Bible\_, pp. 483,

484.]

[Footnote 143: For a complete historical account of this subject with

full references to all the works upon it, see the Introduction to

Hermann MÃ¼ller's \_Fertilisation of Flowers\_, translated by D'Arcy W.

Thompson.]

[Footnote 144: For the full detail of his experiments, see \_Cross-and

Self-Fertilisation of Plants\_, 1876.]

[Footnote 145: See Darwin's \_Fertilisation of Orchids\_ for the many

extraordinary and complex arrangements in these plants.]

[Footnote 146: The English reader may consult Sir John Lubbock's

\_British Wild Flowers in Relation to Insects\_, and H. MÃ¼ller's great and

original work, \_The Fertilisation of Flowers\_.]

[Footnote 147: MÃ¼ller's \_Fertilisation of Flowers\_, p. 248.]

[Footnote 148: "Alpenblumen," by D.H. MÃ¼ller. See \_Nature\_, vol. xxiii.

p. 333.]

[Footnote 149: This peculiarity of local distribution of colour in

flowers may be compared, as regards its purpose, with the recognition

colours of animals. Just as these latter colours enable the sexes to

recognise each other, and thus avoid sterile unions of distinct species,

so the distinctive form and colour of each species of flower, as

compared with those that usually grow around it, enables the fertilising

insects to avoid carrying the pollen of one flower to the stigma of a

distinct species.]

[Footnote 150: See H. MÃ¼ller's \_Fertilisation of Flowers\_, p. 18.]

[Footnote 151: The above examples are taken from Rev. G. Henslow's paper

on "Self-Fertilisation of Plants," in \_Trans. Linn. Soc.\_ Second series,

\_Botany\_, vol. i. pp. 317-398, with plate. Mr. H.O. Forbes has shown

that the same thing occurs among tropical orchids, in his paper "On the

Contrivances for insuring Self-Fertilisation in some Tropical Orchids,"

\_Journ. Linn. Soc.\_, xxi. p. 538.]

[Footnote 152: These are the numbers given by Darwin, but I am informed

by Mr. Hemsley that many additions have been since made to the list, and

that cleistogamic flowers probably occur in nearly all the natural

orders.]

[Footnote 153: For a full account of cleistogamic flowers, see Darwin's

\_Forms of Flowers\_, chap. viii.]

[Footnote 154: Henslow's "Self-Fertilisation," \_Trans. Linn. Soc.\_

Second series, \_Botany\_, vol. i. p. 391.]

[Footnote 155: The Rev. George Henslow, in his \_Origin of Floral

Structures\_, says: "There is little doubt but that all wind-fertilised

angiosperms are degradations from insect-fertilised flowers....

\_Poterium sanguisorba\_ is anemophilous; and \_Sanguisorba officinalis\_

presumably was so formerly, but has reacquired an entomophilous habit;

the whole tribe Poterieae being, in fact, a degraded group which has

descended from Potentilleae. Plantains retain their corolla but in a

degraded form. Junceae are degraded Lilies; while Cyperaceae and

Gramineae among monocotyledons may be ranked with Amentiferae among

dicotyledons, as representing orders which have retrograded very far

from the entomophilous forms from which they were possibly and probably

descended" (p. 266).

"The genus Plantago, like \_Thalictrum minus\_, Poterium, and others, well

illustrate the change from an entomophilous to the anemophilous state.

\_P. lanceolata\_ has polymorphic flowers, and is visited by

pollen-seeking insects, so that it can be fertilised either by insects

or the wind. \_P. media\_ illustrates transitions in point of structure,

as the filaments are pink, the anthers motionless, and the pollen grains

aggregated, and it is regularly visited by \_Bombus terrestris\_. On the

other hand, the slender filaments, versatile anthers, powdery pollen,

and elongated protogynous style are features of other species indicating

anemophily; while the presence of a degraded corolla shows its ancestors

to have been entomophilous. \_P. media\_, therefore, illustrates, not a

primitive entomophilous condition, but a return to it; just as is the

case with \_Sanguisorba officinalis\_ and \_Salix Caprea\_; but these show

no capacity of restoring the corolla, the attractive features having to

be borne by the calyx, which is purplish in Sanguisorba, by the pink

filaments of Plantago, and by the yellow anthers in the Sallow willow"

(p. 271).

"The interpretation, then, I would offer of inconspicuousness and all

kinds of degradations is the exact opposite to that of conspicuousness

and great differentiations; namely, that species with minute flowers,

rarely or never visited by insects, and habitually self-fertilised, have

primarily arisen through the neglect of insects, and have in consequence

assumed their present floral structures" (p. 282).

In a letter just received from Mr. Henslow, he gives a few additional

illustrations of his views, of which the following are the most

important: "Passing to Incompletae, the orders known collectively as

'Cyclospermeae' are related to Caryophylleae; and to my mind are

degradations from it, of which Orache is anemophilous. Cupuliferae have

an inferior ovary and rudimentary calyx-limb on the top. These, as far

as I know, cannot be interpreted except as degradations. The whole of

Monocotyledons appear to me (from anatomical reasons especially) to be

degradations from Dicotyledons, and primarily through the agency of

growth in water. Many subsequently became terrestrial, but retained the

effects of their primitive habitat through heredity. The 3-merous [sic]

perianth of grasses, the parts of the flower being in whorls, point to a

degradation from a sub-liliaceous condition."

Mr. Henslow informs me that he has long held these views, but, as far as

he knows, alone. Mr. Grant Allen, however, set forth a similar theory in

his \_Vignettes from Nature\_ (p. 15) and more fully in \_The Colours of

Flowers\_ (chap. v.), where he develops it fully and uses similar

arguments to those of Mr. Henslow.]

[Footnote 156: H. MÃ¼ller gives ample proof of this in his \_Fertilisation

of Flowers\_.]

[Footnote 157: \_Cross-and Self-Fertilisation\_, p. 27.]

[Footnote 158: \_Animals and Plants\_, vol. ii. p. 145.]

[Footnote 159: MÃ¼ller's \_Fertilisation of Flowers\_, pp. 448, 455. Other

cases of recent degradation and readaptation to insect-fertilisation are

given by Professor Henslow (see footnote, p. 324).]

[Footnote 160: \_The Colour Sense\_, by Grant Allen, p. 95.]

[Footnote 161: \_The Colour Sense\_, chap. ix.]

[Footnote 162: See \_Origin of Species\_, sixth edition, p. 220.]

CHAPTER XII

THE GEOGRAPHICAL DISTRIBUTION OF ORGANISMS

The facts to be explained--The conditions which have determined

distribution--The permanence of oceans--Oceanic and continental

areas--Madagascar and New Zealand--The teachings of the

thousand-fathom line--The distribution of marsupials--The

distribution of tapirs--Powers of dispersal as illustrated by

insular organisms--Birds and insects at sea--Insects at great

altitudes--The dispersal of plants--Dispersal of seeds by the

wind--Mineral matter carried by the wind--Objections to the

theory of wind-dispersal answered--Explanation of north

temperate plants in the southern hemisphere--No proof of

glaciation in the tropics--Lower temperature not needed to

explain the facts--Concluding remarks.

The theory which we may now take as established--that all the existing

forms of life have been derived from other forms by a natural process of

descent with modification, and that this same process has been in action

during past geological time--should enable us to give a rational account

not only of the peculiarities of form and structure presented by animals

and plants, but also of their grouping together in certain areas, and

their general distribution over the earth's surface.

In the absence of any exact knowledge of the facts of distribution, a

student of the theory of evolution might naturally anticipate that all

groups of allied organisms would be found in the same region, and that,

as he travelled farther and farther from any given centre, the forms of

life would differ more and more from those which prevailed at the

starting-point, till, in the remotest regions to which he could

penetrate, he would find an entirely new assemblage of animals and

plants, altogether unlike those with which he was familiar. He would

also anticipate that diversities of climate would always be associated

with a corresponding diversity in the forms of life.

Now these anticipations are to a considerable extent justified.

Remoteness on the earth's surface is usually an indication of diversity

in the fauna and flora, while strongly contrasted climates are always

accompanied by a considerable contrast in the forms of life. But this

correspondence is by no means exact or proportionate, and the converse

propositions are often quite untrue. Countries which are near to each

other often differ radically in their animal and vegetable productions;

while similarity of climate, together with moderate geographical

proximity, are often accompanied by marked diversities in the prevailing

forms of life. Again, while many groups of animals--genera, families,

and sometimes even orders--are confined to limited regions, most of the

families, many genera, and even some species are found in every part of

the earth. An enumeration of a few of these anomalies will better

illustrate the nature of the problem we have to solve.

As examples of extreme diversity, notwithstanding geographical

proximity, we may adduce Madagascar and Africa, whose animal and

vegetable productions are far less alike than are those of Great Britain

and Japan at the remotest extremities of the great northern continent;

while an equal, or perhaps even a still greater, diversity exists

between Australia and New Zealand. On the other hand, Northern Africa

and South Europe, though separated by the Mediterranean Sea, have faunas

and floras which do not differ from each other more than do the various

countries of Europe. As a proof that similarity of climate and general

adaptability have had but a small part in determining the forms of life

in each country, we have the fact of the enormous increase of rabbits

and pigs in Australia and New Zealand, of horses and cattle in South

America, and of the common sparrow in North America, though in none of

these cases are the animals natives of the countries in which they

thrive so well. And lastly, in illustration of the fact that allied

forms are not always found in adjacent regions, we have the tapirs,

which are found only on opposite sides of the globe, in tropical America

and the Malayan Islands; the camels of the Asiatic deserts, whose

nearest allies are the llamas and alpacas of the Andes; and the

marsupials, only found in Australia and on the opposite side of the

globe, in America. Yet, again, although mammalia may be said to be

universally distributed over the globe, being found abundantly on all

the continents and on a great many of the larger islands, yet they are

entirely wanting in New Zealand, and in a considerable number of other

islands which are, nevertheless, perfectly able to support them when

introduced.

Now most of these difficulties can be solved by means of well-known

geographical and geological facts. When the productions of remote

countries resemble each other, there is almost always continuity of land

with similarity of climate between them. When adjacent countries differ

greatly in their productions, we find them separated by a sea or strait

whose great depth is an indication of its antiquity or permanence. When

a group of animals inhabits two countries or regions separated by wide

oceans, it is found that in past geological times the same group was

much more widely distributed, and may have reached the countries it

inhabits from an intermediate region in which it is now extinct. We

know, also, that countries now united by land were divided by arms of

the sea at a not very remote epoch; while there is good reason to

believe that others now entirely isolated by a broad expanse of sea were

formerly united and formed a single land area. There is also another

important factor to be taken account of in considering how animals and

plants have acquired their present peculiarities of

distribution,--changes of climate. We know that quite recently a glacial

epoch extended over much of what are now the temperate regions of the

northern hemisphere, and that consequently the organisms which inhabit

those parts must be, comparatively speaking, recent immigrants from more

southern lands. But it is a yet more important fact that, down to middle

Tertiary times at all events, an equable temperate climate, with a

luxuriant vegetation, extended to far within the arctic circle, over

what are now barren wastes, covered for ten months of the year with snow

and ice. The arctic zone has, therefore, been in past times capable of

supporting almost all the forms of life of our temperate regions; and we

must take account of this condition of things whenever we have to

speculate on the possible migrations of organisms between the old and

new continents.

\_The Conditions which have determined Distribution.\_

When we endeavour to explain in detail the facts of the existing

distribution of organic beings, we are confronted by several preliminary

questions, upon the solution of which will depend our treatment of the

phenomena presented to us. Upon the theory of descent which we have

adopted, all the different species of a genus, as well as all the genera

which compose a family or higher group, have descended from some common

ancestor, and must therefore, at some remote epoch, have occupied the

same area, from which their descendants have spread to the regions they

now inhabit. In the numerous cases in which the same group now occupies

countries separated by oceans or seas, by lofty mountain-chains, by wide

deserts, or by inhospitable climates, we have to consider how the

migration which must certainly have taken place has been effected. It is

possible that during some portion of the time which has elapsed since

the origin of the group the interposing barriers have not been in

existence; or, on the other hand, the particular organisms we are

dealing with may have the power of overpassing the barriers, and thus

reaching their present remote dwelling-places. As this is really the

fundamental question of distribution on which the solution of all its

more difficult problems depends, we have to inquire, in the first place,

what is the nature of, and what are the limits to, the changes of the

earth's surface, especially during the Tertiary and latter part of the

Secondary periods, as it was during those periods that most of the

existing types of the higher animals and plants came into existence;

and, in the next place, what are the extreme limits of the powers of

dispersal possessed by the chief groups of animals and plants. We will

first consider the question of barriers, more especially those formed by

seas and oceans.

\_The Permanence of Oceans.\_

It was formerly a very general belief, even amongst geologists, that the

great features of the earth's surface, no less than the smaller ones,

were subject to continual mutations, and that during the course of

known geological time the continents and great oceans had again and

again changed places with each other. Sir Charles Lyell, in the last

edition of his \_Principles of Geology\_ (1872), said: "Continents,

therefore, although permanent for whole geological epochs, shift their

positions entirely in the course of ages;" and this may be said to have

been the orthodox opinion down to the very recent period when, by means

of deep-sea soundings, the nature of the ocean bottom was made known.

The first person to throw doubt on this view appears to have been the

veteran American geologist, Professor Dana. In 1849, in the Report of

Wilke's Exploring Expedition, he adduced the argument against a former

continent in the Pacific during the Tertiary period, from the absence of

all native quadrupeds. In 1856, in articles in the \_American Journal\_,

he discussed the development of the American continent, and argued for

its general permanence; and in his \_Manual of Geology\_ in 1863 and later

editions, the same views were more fully enforced and were latterly

applied to all continents. Darwin, in his \_Journal of Researches\_,

published in 1845, called attention to the fact that all the small

islands far from land in the Pacific, Indian, and Atlantic Oceans are

either of coralline or volcanic formation. He excepted, however, the

Seychelles and St. Paul's rocks; but the former have since been shown to

be no exception, as they consist entirely of coral rock; and although

Darwin himself spent a few hours on St. Paul's rocks on his outward

voyage in the \_Beagle\_, and believed he had found some portions of them

to be of a "cherty," and others of a "felspathic" nature, this also has

been shown to be erroneous, and the careful examination of the rocks by

the AbbÃ© Renard clearly proves them to be wholly of volcanic

origin.[163] We have, therefore, at the present time, absolutely no

exception whatever to the remarkable fact that all the oceanic islands

of the globe are either of volcanic or coral formation; and there is,

further, good reason to believe that those of the latter class in every

case rest upon a volcanic foundation.

In his \_Origin of Species\_, Darwin further showed that no true oceanic

island had any native mammals or batrachia when first discovered, this

fact constituting the test of the class to which an island belongs;

whence he argued that none of them had ever been connected with

continents, but all had originated in mid-ocean. These considerations

alone render it almost certain that the areas now occupied by the great

oceans have never, during known geological time, been occupied by

continents, since it is in the highest degree improbable that every

fragment of those continents should have completely disappeared, and

have been replaced by volcanic islands rising out of profound oceanic

abysses; but recent research into the depth of the oceans and the nature

of the deposits now forming on their floors, adds greatly to the

evidence in this direction, and renders it almost a certainty that they

represent very ancient if not primaeval features of the earth's surface.

A very brief outline of the nature of this evidence will be now given.

The researches of the \_Challenger\_ expedition into the nature of the

sea-bottom show, that the whole of the land debris brought down by

rivers to the ocean (with the exception of pumice and other floating

matter), is deposited comparatively near to the shores, and that the

fineness of the material is an indication of the distance to which it

has been carried. Everything in the nature of gravel and sand is laid

down within a very few miles of land, only the finer muddy sediments

being carried out for 20 or 50 miles, and the very finest of all, under

the most favourable conditions, rarely extending beyond 150, or at the

utmost, 300 miles from land into the deep ocean.[164] Beyond these

distances, and covering the entire ocean floor, are various oozes formed

wholly from the debris of marine organisms; while intermingled with

these are found various volcanic products which have been either carried

through the air or floated on the surface, and a small but perfectly

recognisable quantity of meteoric matter. Ice-borne rocks are also found

abundantly scattered over the ocean bottom within a definite distance of

the arctic and antarctic circles, clearly marking out the limit of

floating icebergs in recent geological times.

Now the whole series of marine stratified rocks, from the earliest

Palaeozoic to the most recent Tertiary beds, consist of materials

closely corresponding to the land debris now being deposited within a

narrow belt round the shores of all continents; while no rocks have been

found which can be identified with the various oozes now forming in the

deep abysses of the ocean. It follows, therefore, that all the

geological formations have been formed in comparatively shallow water,

and always adjacent to the continental land of the period. The great

thickness of some of the formations is no indication of a deep sea, but

only of slow subsidence during the time that the deposition was in

progress. This view is now adopted by many of the most experienced

geologists, especially by Dr. Archibald Geikie, Director of the

Geological Survey of Great Britain, who, in his lecture on "Geographical

Evolution," says: "From all this evidence we may legitimately conclude

that the present land of the globe, though consisting in great measure

of marine formations, has never lain under the deep sea; but that its

site must always have been near land. Even its thick marine limestones

are the deposits of comparatively shallow water."[165]

But besides these geological and physical considerations, there is a

mechanical difficulty in the way of repeated change of position of

oceans and continents which has not yet received the attention it

deserves. According to the recent careful estimate by Mr. John Murray,

the land area of the globe is to the water area as Â·28 to Â·72. The mean

height of the land above sea-level is 2250 feet, while the mean depth of

the ocean is 14,640 feet. Hence the bulk of dry land is 23,450,000 cubic

miles, and that of the waters of the ocean 323,800,000 cubic miles; and

it follows that if the whole of the solid matter of the earth's surface

were reduced to one level, it would be everywhere covered by an ocean

about two miles deep. The accompanying diagram will serve to render

these figures more intelligible. The length of the sections of land and

ocean are in the proportion of their respective areas, while the mean

height of the land and the mean depth of the ocean are exhibited on a

greatly increased vertical scale. If we considered the continents and

their adjacent oceans separately they would differ a little, but not

very materially, from this diagram; in some cases the proportion of land

to ocean would be a little greater, in others a little less.

[Illustration: FIG. 32.]

Now, if we try to imagine a process of elevation and depression by which

the sea and land shall completely change places, we shall be met by

insuperable difficulties. We must, in the first place, assume a general

equality between elevation and subsidence during any given period,

because if the elevation over any extensive continental area were not

balanced by some subsidence of approximately equal amount, an

unsupported hollow would be left under the earth's crust. Let us now

suppose a continental area to sink, and an adjacent oceanic area to

rise, it will be seen that the greater part of the land will disappear

long before the new land has approached the surface of the ocean. This

difficulty will not be removed by supposing a portion of a continent to

subside, and the immediately adjacent portion of the ocean on the other

side of the continent to rise, because in almost every case we find that

within a comparatively short distance from the shores of all existing

continents, the ocean floor sinks rapidly to a depth of from 2000 to

3000 fathoms, and maintains a similar depth, generally speaking, over a

large portion of the oceanic areas. In order, therefore, that any area

of continental extent be upraised from the great oceans, there must be a

subsidence of a land area five or six times as great, unless it can be

shown that an extensive elevation of the ocean floor up to and far

above the surface could occur without an equivalent depression

elsewhere. The fact that the waters of the ocean are sufficient to cover

the whole globe to a depth of two miles, is alone sufficient to indicate

that the great ocean basins are permanent features of the earth's

surface, since any process of alternation of these with the land areas

would have been almost certain to result again and again in the total

disappearance of large portions, if not of all, of the dry land of the

globe. But the continuity of terrestrial life since the Devonian and

Carboniferous periods, and the existence of very similar forms in the

corresponding deposits of every continent--as well as the occurrence of

sedimentary rocks, indicating the proximity of land at the time of their

deposit, over a large portion of the surface of all the continents, and

in every geological period--assure us that no such disappearance has

ever occurred.

\_Oceanic and Continental Areas.\_

When we speak of the permanence of oceanic and continental areas as one

of the established facts of modern research, we do not mean that

existing continents and oceans have always maintained the exact areas

and outlines that they now present, but merely, that while all of them

have been undergoing changes in outline and extent from age to age, they

have yet maintained substantially the same positions, and have never

actually changed places with each other. There are, moreover, certain

physical and biological facts which enable us to mark out these areas

with some confidence.

We have seen that there are a large number of islands which may be

classed as oceanic, because they have never formed parts of continents,

but have originated in mid-ocean, and have derived their forms of life

by migration across the sea. Their peculiarities are seen to be very

marked in comparison with those islands which there is good reason to

believe are really fragments of more extensive land areas, and are hence

termed "continental." These continental islands consist in every case of

a variety of stratified rocks of various ages, thus corresponding

closely with the usual structure of continents; although many of the

islands are small like Jersey or the Shetland Islands, or far from

continental land like the Falkland Islands or New Zealand. They all

contain indigenous mammalia or batrachia, and generally a much greater

variety of birds, reptiles, insects, and plants, than do the oceanic

islands. From these various characteristics we conclude that they have

all once formed parts of continents, or at all events of much larger

land areas, and have become isolated, either by subsidence of the

intervening land or by the effects of long-continued marine denudation.

Now, if we trace the thousand-fathom line around all our existing

continents we find that, with only two exceptions, every island which

can be classed as "continental" falls within this line, while all that

lie beyond it have the undoubted characteristics of "oceanic" islands.

We, therefore, conclude that the thousand-fathom line marks out,

approximately, the "continental area,"--that is, the limits within which

continental development and change throughout known geological time have

gone on. There may, of course, have been some extensions of land beyond

this limit, while some areas within it may always have been ocean; but

so far as we have any direct evidence, this line may be taken to mark

out, approximately, the most probable boundary between the "continental

area," which has always consisted of land and shallow sea in varying

proportions, and the great oceanic basins, within the limits of which

volcanic activity has been building up numerous islands, but whose

profound depths have apparently undergone little change.

\_Madagascar and New Zealand.\_

The two exceptions just referred to are Madagascar and New Zealand, and

all the evidence goes to show that in these cases the land connection

with the nearest continental area was very remote in time. The

extraordinary isolation of the productions of Madagascar--almost all the

most characteristic forms of mammalia, birds, and reptiles of Africa

being absent from it--renders it certain that it must have been

separated from that continent very early in the Tertiary, if not as far

back as the latter part of the Secondary period; and this extreme

antiquity is indicated by a depth of considerably more than a thousand

fathoms in the Mozambique Channel, though this deep portion is less than

a hundred miles wide between the Comoro Islands and the mainland.[166]

Madagascar is the only island on the globe with a fairly rich mammalian

fauna which is separated from a continent by a depth greater than a

thousand fathoms; and no other island presents so many peculiarities in

these animals, or has preserved so many lowly organised and archaic

forms. The exceptional character of its productions agrees exactly with

its exceptional isolation by means of a very deep arm of the sea.

New Zealand possesses no known mammals and only a single species of

batrachian; but its geological structure is perfectly continental. There

is also much evidence that it does possess one mammal, although no

specimens have been yet obtained.[167] Its reptiles and birds are highly

peculiar and more numerous than in any truly oceanic island. Now the sea

which directly separates New Zealand from Australia is more than 2000

fathoms deep, but in a north-west direction there is an extensive bank

under 1000 fathoms, extending to and including Lord Howe's Island, while

north of this are other banks of the same depth, approaching towards a

submarine extension of Queensland on the one hand, and New Caledonia on

the other, and altogether suggestive of a land union with Australia at

some very remote period. Now the peculiar relations of the New Zealand

fauna and flora with those of Australia and of the tropical Pacific

Islands to the northward indicate such a connection, probably during the

Cretaceous period; and here, again, we have the exceptional depth of the

dividing sea and the form of the ocean bottom according well with the

altogether exceptional isolation of New Zealand, an isolation which has

been held by some naturalists to be great enough to justify its claim to

be one of the primary Zoological Regions.

\_The Teachings of the Thousand-Fathom Line.\_

If now we accept the annexed map as showing us approximately how far

beyond their present limits our continents may have extended during any

portion of the Tertiary and Secondary periods, we shall obtain a

foundation of inestimable value for our inquiries into those migrations

of animals and plants during past ages which have resulted in their

present peculiarities of distribution. We see, for instance, that the

South American and African continents have always been separated by

nearly as wide an ocean as at present, and that whatever similarities

there may be in their productions must be due to the similar forms

having been derived from a common origin in one of the great northern

continents. The radical difference between the higher forms of life of

the two continents accords perfectly with their permanent separation. If

there had been any direct connection between them during Tertiary times,

we should hardly have found the deep-seated differences between the

Quadrumana of the two regions--no family even being common to both; nor

the peculiar Insectivora of the one continent, and the equally peculiar

Edentata of the other. The very numerous families of birds quite

peculiar to one or other of these continents, many of which, by their

structural isolation and varied development of generic and specific

forms, indicate a high antiquity, equally suggest that there has been no

near approach to a land connection during the same epoch.

Looking to the two great northern continents, we see indications of a

possible connection between them both in the North Atlantic and the

North Pacific oceans; and when we remember that from middle Tertiary

times backward--so far as we know continuously to the earliest

Palaeozoic epoch--a temperate and equable climate, with abundant woody

vegetation, prevailed up to and within the arctic circle, we see what

facilities may have been afforded for migration from one continent to

the other, sometimes between America and Europe, sometimes between

America and Asia. Admitting these highly probable connections, no

bridging of the Atlantic in more southern latitudes (of which there is

not a particle of evidence) will have been necessary to account for all

the intermigration that has occurred between the two continents. If, on

the other hand, we remember how long must have been the route, and how

diverse must always have been the conditions between the more northern

and the more southern portions of the American and Euro-Asiatic

continents, we shall not be surprised that many widespread forms in

either continent have not crossed into the other; and that while the

skunks (Mephitis), the pouched rats (Saccomyidae), and the turkeys

(Meleagris) are confined to America, the pigs and the hedgehogs, the

true flycatchers and the pheasants are found only in the Euro-Asiatic

continent. But, just as there have been periods which facilitated

intermigration between America and the Old World, there have almost

certainly been periods, perhaps of long duration even geologically, when

these continents have been separated by seas as wide as, or even wider

than, those of the present day; and thus may be explained such curious

anomalies as the origination of the camel-tribe in America, and its

entrance into Asia in comparatively recent Tertiary times, while the

introduction of oxen and bears into America from the Euro-Asiatic

continent appears to have been equally recent.[168]

We shall find on examination that this view of the general permanence of

the oceanic and continental areas, with constant minor fluctuations of

land and sea over the whole extent of the latter, enables us to

understand, and offer a rational explanation of, most of the difficult

problems of geographical distribution; and further, that our power of

doing this is in direct proportion to our acquaintance with the

distribution of fossil forms of life during the Tertiary period. We

must, also, take due note of many other facts of almost equal importance

for a due appreciation of the problems presented for solution, the most

essential being, the various powers of dispersal possessed by the

different groups of animals and plants, the geological antiquity of the

species and genera, and the width and depth of the seas which separate

the countries they, inhabit. A few illustrations will now be given of

the way in which these branches of knowledge enable us to deal with the

difficulties and anomalies that present themselves.

\_The Distribution of Marsupials.\_

This singular and lowly organised type of mammals constitutes almost the

sole representative of the class in Australia and New Guinea, while it

is entirely unknown in Asia, Africa, or Europe. It reappears in America,

where several species of opossums are found; and it was long thought

necessary to postulate a direct southern connection of these distant

countries, in order to account for this curious fact of distribution.

When, however, we look to what is known of the geological history of the

marsupials the difficulty vanishes. In the Upper Eocene deposits of

Western Europe the remains of several animals closely allied to the

American opossums have been found; and as, at this period, a very mild

climate prevailed far up into the arctic regions, there is no difficulty

in supposing that the ancestors of the group entered America from Europe

or Northern Asia during early Tertiary times.

But we must go much further back for the origin of the Australian

marsupials. All the chief types of the higher mammalia were in existence

in the Eocene, if not in the preceding Cretaceous period, and as we find

none of these in Australia, that country must have been finally

separated from the Asiatic continent during the Secondary or Mesozoic

period. Now during that period, in the Upper and the Lower Oolite and in

the still older Trias, the jaw-bones of numerous small mammalia have

been found, forming eight distinct genera, which are believed to have

been either marsupials or some allied lowly forms. In North America

also, in beds of the Jurassic and Triassic formations, the remains of an

equally great variety of these small mammalia have been discovered; and

from the examination of more than sixty specimens, belonging to at least

six distinct genera, Professor Marsh is of opinion that they represent a

generalised type, from which the more specialised marsupials and

insectivora were developed.

From the fact that very similar mammals occur both in Europe and America

at corresponding periods, and in beds which represent a long succession

of geological time, and that during the whole of this time no fragments

of any higher forms have been discovered, it seems probable that both

the northern continents (or the larger portion of their area) were then

inhabited by no other mammalia than these, with perhaps other equally

low types. It was, probably, not later than the Jurassic age when some

of these primitive marsupials were able to enter Australia, where they

have since remained almost completely isolated; and, being free from

the competition of higher forms, they have developed into the great

variety of types we now behold there. These occupy the place, and have

to some extent acquired the form and structure of distinct orders of the

higher mammals--the rodents, the insectivora, and the carnivora,--while

still preserving the essential characteristics and lowly organisation of

the marsupials. At a much later period--probably in late Tertiary

times--the ancestors of the various species of rats and mice which now

abound in Australia, and which, with the aerial bats, constitute its

only forms of placental mammals, entered the country from some of the

adjacent islands. For this purpose a land connection was not necessary,

as these small creatures might easily be conveyed among the branches or

in the crevices of trees uprooted by floods and carried down to the sea,

and then floated to a shore many miles distant. That no actual land

connection with, or very close approximation to, an Asiatic island has

occurred in recent times, is sufficiently proved by the fact that no

squirrel, pig, civet, or other widespread mammal of the Eastern

hemisphere has been able to reach the Australian continent.

\_The Distribution of Tapirs.\_

These curious animals form one of the puzzles of geographical

distribution, being now confined to two very remote regions of the

globe--the Malay Peninsula and adjacent islands of Sumatra and Borneo,

inhabited by one species, and tropical America, where there are three or

four species, ranging from Brazil to Ecuador and Guatemala. If we

considered these living forms only, we should be obliged to speculate on

enormous changes of land and sea in order that these tropical animals

might have passed from one country to the other. But geological

discoveries have rendered all such hypothetical changes unnecessary.

During Miocene and Pliocene times tapirs abounded over the whole of

Europe and Asia, their remains having been found in the tertiary

deposits of France, India, Burmah, and China. In both North and South

America fossil remains of tapirs occur only in caves and deposits of

Post-Pliocene age, showing that they are comparatively recent immigrants

into that continent. They perhaps entered by the route of Kamchatka and

Alaska, where the climate, even now so much milder and more equable than

on the north-east of America, might have been warm enough in late

Pliocene times to have allowed the migration of these animals. In Asia

they were driven southwards by the competition of numerous higher and

more powerful forms, but have found a last resting-place in the swampy

forests of the Malay region.

\_What these Facts Prove.\_

Now these two cases, of the marsupials and the tapirs, are in the

highest degree instructive, because they show us that, without any

hypothetical bridging of deep oceans, and with only such changes of sea

and land as are indicated by the extent of the comparatively shallow

seas surrounding and connecting the existing continents, we are able to

account for the anomaly of allied forms occurring only in remote and

widely separated areas. These examples really constitute crucial tests,

because, of all classes of animals, mammalia are least able to surmount

physical barriers. They are obviously unable to pass over wide arms of

the sea, while the necessity for constant supplies of food and water

renders sandy deserts or snow-clad plains equally impassable. Then,

again, the peculiar kinds of food on which alone many of them can

subsist, and their liability to the attacks of other animals, put a

further check upon their migrations. In these respects almost all other

organisms have great advantages over mammals. Birds can often fly long

distances, and can thus cross arms of the sea, deserts, or mountain

ranges; insects not only fly, but are frequently carried great distances

by gales of wind, as shown by the numerous cases of their visits to

ships hundreds of miles from land. Reptiles, though slow of movement,

have advantages in their greater capacity for enduring hunger or thirst,

their power of resisting cold or drought in a state of torpidity, and

they have also some facilities for migration across the sea by means of

their eggs, which may be conveyed in crevices of timber or among masses

of floating vegetable matter. And when we come to the vegetable kingdom,

the means of transport are at their maximum, numbers of seeds having

special adaptations for being carried by mammalia or birds, and for

floating in the water, or through the air, while many are so small and

so light that there is practically no limit to the distances they may be

carried by gales and hurricanes.

We may, therefore, feel quite certain that the means of distribution

that have enabled the larger mammalia to reach the most remote regions

from a common starting-point, will be at least as efficacious, and

usually far more efficacious, with all other land animals and plants;

and if in every case the existing distribution of this class can be

explained on the theory of oceanic and continental permanence, with the

limited changes of sea and land already referred to, no valid objections

can be taken against this theory founded on anomalies of distribution in

other orders. Yet nothing is more common than for students of this or

that group to assort that the theory of oceanic permanence is quite

inconsistent with the distribution of its various species and genera.

Because a few Indian genera and closely allied species of birds are

found in Madagascar, a land termed "Lemuria" has been supposed to have

united the two countries during a comparatively recent geological epoch;

while the similarity of fossil plants and reptiles, from the Permian and

Miocene formations of India and South Africa, has been adduced as

further evidence of this connection. But there are also genera of

snakes, of insects, and of plants, common to Madagascar and South

America only, which have been held to necessitate a direct land

connection between these countries. These views evidently refute

themselves, because any such land connections must have led to a far

greater similarity in the productions of the several countries than

actually exists, and would besides render altogether inexplicable the

absence of all the chief types of African and Indian mammalia from

Madagascar, and its marvellous individuality in every department of the

organic world.[169]

\_Powers of Dispersal as illustrated by Insular Organisms.\_

Having arrived at the conclusion that our existing oceans have remained

practically unaltered throughout the Tertiary and Secondary periods of

geology, and that the distribution of the mammalia is such as might

have been brought about by their known powers of dispersal, and by such

changes of land and sea as have probably or certainly occurred, we are,

of course, restricted to similar causes to explain the much wider and

sometimes more eccentric distribution of other classes of animals and of

plants. In doing so, we have to rely partly on direct evidence of

dispersal, afforded by the land organisms that have been observed far

out at sea, or which have taken refuge on ships, as well as by the

periodical visitants to remote islands; but very largely on indirect

evidence, afforded by the frequent presence of certain groups on remote

oceanic islands, which some ancestral forms must, therefore, have

reached by transmission across the ocean from distant lands.

\_Birds.\_

These vary much in their powers of flight, and their capability of

traversing wide seas and oceans. Many swimming and wading birds can

continue long on the wing, fly swiftly, and have, besides, the power of

resting safely on the surface of the water. These would hardly be

limited by any width of ocean, except for the need of food; and many of

them, as the gulls, petrels, and divers, find abundance of food on the

surface of the sea itself. These groups have a wide distribution

\_across\_ the oceans; while waders--especially plovers, sandpipers,

snipes, and herons--are equally cosmopolitan, travelling \_along\_ the

coasts of all the continents, and across the narrow seas which separate

them. Many of these birds seem unaffected by climate, and as the

organisms on which they feed are equally abundant on arctic, temperate,

and tropical shores, there is hardly any limit to the range even of some

of the species.

Land-birds are much more restricted in their range, owing to their

usually limited powers of flight, their inability to rest on the surface

of the sea or to obtain food from it, and their greater specialisation,

which renders them less able to maintain themselves in the new countries

they may occasionally reach. Many of them are adapted to live only in

woods, or in marshes, or in deserts; they need particular kinds of food

or a limited range of temperature; and they are adapted to cope only

with the special enemies or the particular group of competitors among

which they have been developed. Such birds as these may pass again and

again to a new country, but are never able to establish themselves in

it; and it is this organic barrier, as it is termed, rather than any

physical barrier, which, in many cases, determines the presence of a

species in one area and its absence from another. We must always

remember, therefore, that, although the presence of a species in a

remote oceanic island clearly proves that its ancestors must at one time

have found their way there, the absence of a species does not prove the

contrary, since it also may have reached the island, but have been

unable to maintain itself, owing to the inorganic or organic conditions

not being suitable to it. This general principle applies to all classes

of organisms, and there are many striking illustrations of it. In the

Azores there are eighteen species of land-birds which are permanent

residents, but there are also several others which reach the islands

almost every year after great storms, but have never been able to

establish themselves. In Bermuda the facts are still more striking,

since there are only ten species of resident birds, while no less than

twenty other species of land-birds and more than a hundred species of

waders and aquatics are frequent visitors, often in great numbers, but

are never able to establish themselves. On the same principle we account

for the fact that, of the many continental insects and birds that have

been let loose, or have escaped from confinement, in this country,

hardly one has been able to maintain itself, and the same phenomenon is

still more striking in the case of plants. Of the thousands of hardy

plants which grow easily in our gardens, very few have ever run wild,

and when the experiment is purposely tried it invariably fails. Thus A.

de Candolle informs us that several botanists of Paris, Geneva, and

especially of Montpellier, have sown the seeds of many hundreds of

species of exotic hardy plants, in what appeared to be the most

favourable situations, but that in hardly a single case has any one of

them become naturalised.[170] Still more, then, in plants than in

animals the absence of a species does not prove that it has never

reached the locality, but merely that it has not been able to maintain

itself in competition with the native productions. In other cases, as

we have seen, facts of an exactly opposite nature occur. The rat, the

pig, and the rabbit, the water-cress, the clover, and many other plants,

when introduced into New Zealand, nourish exceedingly, and even

exterminate their native competitors; so that in these cases we may feel

sure that the species in question did not exist in New Zealand simply

because they had been unable to reach that country by their natural

means of dispersal. I will now give a few cases, in addition to those

recorded in my previous works, of birds and insects which have been

observed far from any land.

\_Birds and Insects at Sea.\_

Captain D. Fullarton of the ship \_Timaru\_ recorded in his log the

occurrence of a great number of small land-birds about the ship on 15th

March 1886, when in Lat. 48Â° 31' N., Long. 8Â° 16' W. He says: "A great

many small land-birds about us; put about sixty into a coop, evidently

tired out." And two days later, 17th March, "Over fifty of the birds

cooped on 15th died, though fed. Sparrows, finches, water-wagtails, two

small birds, name unknown, one kind like a linnet, and a large bird like

a starling. In all there have been on board over seventy birds, besides

some that hovered about us for some time and then fell into the sea

exhausted." Easterly winds and severe weather were experienced at the

time.[171] The spot where this remarkable flight of birds was met with

is about 160 miles due west of Brest, and this is the least distance the

birds must have been carried. It is interesting to note that the

position of the ship is nearly in the line from the English and French

coasts to the Azores, where, after great storms, so many bird stragglers

arrive annually. These birds were probably blown out to sea during their

spring migration along the south coast of England to Wales and Ireland.

During the autumnal migration, however, great flocks of

birds--especially starlings, thrushes, and fieldfares--have been

observed every year flying out to sea from the west coast of Ireland,

almost the whole of which must perish. At the Nash Lighthouse, in the

Bristol Channel on the coast of Glamorganshire, an enormous number of

small birds were observed on 3d September, including nightjars,

buntings, white-throats, willow-wrens, cuckoos, house-sparrows, robins,

wheatears, and blackbirds. These had probably crossed from

Somersetshire, and had they been caught by a storm the larger portion of

them must have been blown out to sea.[172]

These facts enable us to account sufficiently well for the birds of

oceanic islands, the number and variety of which are seen to be

proportionate to their facilities for reaching the island and

maintaining themselves in it. Thus, though more birds yearly reach

Bermuda than the Azores, the number of residents in the latter islands

is much larger, due to the greater extent of the islands, their number,

and their more varied surface. In the Galapagos the land-birds are still

more numerous, due in part to their larger area and greater proximity to

the continent, but chiefly to the absence of storms, so that the birds

which originally reached the islands have remained long isolated and

have developed into many closely allied species adapted to the special

conditions. All the species of the Galapagos but one are peculiar to the

islands, while the Azores possess only one peculiar species, and Bermuda

none--a fact which is clearly due to the continual immigration of fresh

individuals keeping up the purity of the breed by intercrossing. In the

Sandwich Islands, which are extremely isolated, being more than 2000

miles from any continent or large island, we have a condition of things

similar to what prevails in the Galapagos, the land-birds, eighteen in

number, being all peculiar, and belonging, except one, to peculiar

genera. These birds have probably all descended from three or four

original types which reached the islands at some remote period, probably

by means of intervening islets that have since disappeared. In St.

Helena we have a degree of permanent isolation which has prevented any

land-birds from reaching the island; for although its distance from the

continent, 1100 miles, is not so great as in the case of the Sandwich

Islands, it is situated in an ocean almost entirely destitute of small

islands, while its position within the tropics renders it free from

violent storms. Neither is there, on the nearest part of the coast of

Africa, a perpetual stream of migrating birds like that which supplies

the innumerable stragglers which every year reach Bermuda and the

Azores.

\_Insects.\_

Winged insects have been mainly dispersed in the same way as birds, by

their power of flight, aided by violent or long-continued winds. Being

so small, and of such low specific gravity, they are occasionally

carried to still greater distances; and thus no islands, however remote,

are altogether without them. The eggs of insects, being often deposited

in borings or in crevices of timber, may have been conveyed long

distances by floating trees, as may the larvae of those species which

feed on wood. Several cases have been published of insects coming on

board ships at great distances from land; and Darwin records having

caught a large grasshopper when the ship was 370 miles from the coast of

Africa, whence the insect had probably come.

In the \_Entomologists' Monthly Magazine\_ for June 1885, Mr. MacLachlan

has recorded the occurrence of a swarm of moths in the Atlantic ocean,

from the log of the ship \_Pleione\_. The vessel was homeward bound from

New Zealand, and in Lat. 6Â° 47' N., Long. 32Â° 50' W., hundreds of moths

appeared about the ship, settling in numbers on the spars and rigging.

The wind for four days previously had been very light from north,

north-west, or north-east, and sometimes calm. The north-east trade wind

occasionally extends to the ship's position at that time of year. The

captain adds that "frequently, in that part of the ocean, he has had

moths and butterflies come on board." The position is 960 miles

south-west of the Cape Verde Islands, and about 440 north-east of the

South American coast. The specimen preserved is Deiopeia pulchella, a

very common species in dry localities in the Eastern tropics, and rarely

found in Britain, but, Mr. MacLachlan thinks, not found in South

America. They must have come, therefore, from the Cape Verde Islands, or

from some parts of the African coast, and must have traversed about a

thousand miles of ocean with the assistance, no doubt, of a strong

north-east trade wind for a great part of the distance. In the British

Museum collection there is a specimen of the same moth caught at sea

during the voyage of the \_Rattlesnake\_, in Lat. 6Â° N., Long. 22-1/2Â°

W., being between the former position and Sierra Leone, thus rendering

it probable that the moths came from that part of the African coast, in

which case the swarm encountered by the \_Pleione\_ must have travelled

more than 1200 miles.

A similar case was recorded by Mr. F.A. Lucas in the American periodical

\_Science\_ of 8th April 1887. He states that in 1870 he met with numerous

moths of many species while at sea in the South Atlantic (Lat. 25Â° S.,

Long. 24Â° W.), about 1000 miles from the coast of Brazil. As this

position is just beyond the south-east trades, the insects may have been

brought from the land by a westerly gale. In the \_Zoologist\_ (1864, p.

8920) is the record of a small longicorn beetle which flew on board a

ship 500 miles off the west coast of Africa. Numerous other cases are

recorded of insects at less distances from land, and, taken in

connection with those already given, they are sufficient to show that

great numbers must be continually carried out to sea, and that

occasionally they are able to reach enormous distances. But the

reproductive powers of insects are so great that all we require, in

order to stock a remote island, is that some few specimens shall reach

it even once in a century, or once in a thousand years.

\_Insects at great Altitudes.\_

Equally important is the proof we possess that insects are often carried

to great altitudes by upward currents of air. Humboldt noticed them up

to heights of 15,000 and 18,000 feet in South America, and Mr. Albert

MÃ¼ller has collected many interesting cases of the same character in

Europe.[173] A moth (Plusia gamma) has been found on the summit of Mont

Blanc; small hymenoptera and moths have been seen on the Pyrenees at a

height of 11,000 feet, while numerous flies and beetles, some of

considerable size, have been caught on the glaciers and snow-fields of

various parts of the Alps. Upward currents of air, whirlwinds and

tornadoes, occur in all parts of the world, and large numbers of insects

are thus carried up into the higher regions of the atmosphere, where

they are liable to be caught by strong winds, and thus conveyed enormous

distances over seas or continents. With such powerful means of

dispersal the distribution of insects over the entire globe, and their

presence in the most remote oceanic islands, offer no difficulties.

\_The Dispersal of Plants.\_

The dispersal of seeds is effected in a greater variety of ways than are

available in the case of any animals. Some fruits or seed-vessels, and

some seeds, will float for many weeks, and after immersion in salt water

for that period the seeds will often germinate. Extreme cases are the

double cocoa-nut of the Seychelles, which has been found on the coast of

Sumatra, about 3000 miles distant; the fruits of the Sapindus saponaria

(soap-berry), which has been brought to Bermuda by the Gulf Stream from

the West Indies, and has grown after a journey in the sea of about 1500

miles; and the West Indian bean, Entada scandens, which reached the

Azores from the West Indies, a distance of full 3000 miles, and

afterwards germinated at Kew. By these means we can account for the

similarity in the shore flora of the Malay Archipelago and most of the

islands of the Pacific; and from an examination of the fruits and seeds,

collected among drift during the voyage of the \_Challenger\_, Mr. Hemsley

has compiled a list of 121 species which are probably widely dispersed

by this means.

A still larger number of species owe their dispersal to birds in several

distinct ways. An immense number of fruits in all parts of the world are

devoured by birds, and have been attractively coloured (as we have

seen), in order to be so devoured, because the seeds pass through the

birds' bodies and germinate where they fall. We have seen how frequently

birds are forced by gales of wind across a wide expanse of ocean, and

thus seeds must be occasionally carried. It is a very suggestive fact,

that all the trees and shrubs in the Azores bear berries or small fruits

which are eaten by birds; while all those which bear larger fruits, or

are eaten chiefly by mammals--such as oaks, beeches, hazels, crabs,

etc.--are entirely wanting. Game-birds and waders often have portions of

mud attached to their feet, and Mr. Darwin has proved by experiment that

such mud frequently contains seeds. One partridge had such a quantity of

mud attached to its foot as to contain seeds from which eighty-two

plants germinated; this proves that a very small portion of mud may

serve to convey seeds, and such an occurrence repeated even at long

intervals may greatly aid in stocking remote islands with vegetation.

Many seeds also adhere to the feathers of birds, and thus, again, may be

conveyed as far as birds are ever carried. Dr. Guppy found a small hard

seed in the gizzard of a Cape Petrel, taken about 550 miles east of

Tristan da Cunha.

\_Dispersal of Seeds by the Wind.\_

In the preceding cases we have been able to obtain direct evidence of

transportal; but although we know that many seeds are specially adapted

to be dispersed by the wind, we cannot obtain direct proof that they are

so carried for hundreds or thousands of miles across the sea, owing to

the difficulty of detecting single objects which are so small and

inconspicuous. It is probable, however, that the wind as an agent of

dispersal is really more effective than any of those we have hitherto

considered, because a very large number of plants have seeds which are

very small and light, and are often of such a form as to facilitate

aerial carriage for enormous distances. It is evident that such seeds

are especially liable to be transported by violent winds, because they

become ripe in autumn at the time when storms are most prevalent, while

they either lie upon the surface of the ground, or are disposed in dry

capsules on the plant ready to be blown away. If inorganic particles

comparable in weight, size, or form with such seeds are carried for

great distances, we may be sure that seeds will also be occasionally

carried in the same way. It will, therefore, be necessary to give a few

examples of wind-carriage of small objects.

On 27th July 1875 a remarkable shower of small pieces of hay occurred at

Monkstown, near Dublin. They appeared floating slowly down from a great

height, as if falling from a dark cloud which hung overhead. The pieces

picked up were wet, and varied from single blades of grass to tufts

weighing one or two ounces. A similar shower occurred a few days earlier

in Denbighshire, and was observed to travel in a direction contrary to

that of the wind in the lower atmosphere.[174] There is no evidence of

the distance from which the hay was brought, but as it had been carried

to a great height, it was in a position to be conveyed to almost any

distance by a violent wind, had such occurred at the time.

\_Mineral Matter carried by the Wind.\_

The numerous cases of sand and volcanic dust being carried enormous

distances through the atmosphere sufficiently prove the importance of

wind as a carrier of solid matter, but unfortunately the matter

collected has not been hitherto examined with a view to determine the

maximum size and weight of the particles. A few facts, however, have

been kindly furnished me by Professor Judd, F.R.S. Some dust which fell

at Genoa on 15th October 1885, and was believed to have been brought

from the African desert, consisted of quartz, hornblende, and other

minerals, and contained particles having a diameter of 1/500 inch, each

weighing 1/200,000 grain. This dust had probably travelled over 600

miles. In the dust from Krakatoa, which fell at Batavia, about 100 miles

distant, during the great eruption, there are many solid particles even

larger than those mentioned above. Some of this dust was given me by

Professor Judd, and I found in it several ovoid particles of a much

larger size, being 1/50 inch long, and 1/70 wide and deep. The dust from

the same eruption, which fell on board the ship \_Arabella\_, 970 miles

from the volcano, also contained solid particles 1/500 inch diameter.

Mr. John Murray of the \_Challenger\_ Expedition writes to me that he

finds in the deep sea deposits 500 and even 700 miles west of the coast

of Africa, rounded particles of quartz, having a diameter of 1/250 inch,

and similar particles are found at equally great distances from the

south-west coasts of Australia; and he considers these to be atmospheric

dust carried to that distance by the wind. Taking the sp. gr. of quartz

at 2.6, these particles would weigh about 1/25,000 grain each. These

interesting facts can, however, by no means be taken as indicating the

extreme limits of the power of wind in carrying solid particles. During

the Krakatoa eruption no gale of special violence occurred, and the

region is one of comparative calms. The grains of quartz found by Mr.

Murray more nearly indicate the limit, but the very small portions of

matter brought up by the dredge, as compared with the enormous areas of

sea-bottom, over which the atmospheric dust must have been scattered,

render it in the highest degree improbable that the maximum limit either

of size of particles, or of distance from land has been reached.

Let us, however, assume that the quartz grains, found by Mr. Murray in

the deep-sea ooze 700 miles from land, give us the extreme limit of the

power of the atmosphere as a carrier of solid particles, and let us

compare with these the weights of some seeds. From a small collection of

the seeds of thirty species of herbaceous plants sent me from Kew, those

in the above table were selected, and small portions of eight of them

carefully weighed in a chemical balance.[175] By counting these portions

I was able to estimate the number of seeds weighing one grain. The three

very minute species, whose numbers are marked with an asterisk (\*), were

estimated by the comparison of their sizes with those of the smaller

weighed seeds.

No| Species. |Approximate | Approximate | Remarks.

| |No. of Seeds| Dimensions. |

| |In one Grain| |

| | | in. in. in. |

1|Draba verna | 1,800 |1/60 x 1/90 x 1/160|Oval, flat.

2|Hypericum perforatum | 520 | 1/30 x 1/80 |Cylindrical.

3|Astilbe rivularis | 4,500 | 1/50 x 1/100 |Elongate, flat, tailed,

| | | | wavy.

4|Saxifraga coriophylla| 750 | 1/40 x 1/75 |Surface rough, adhere

| | | | to the dry capsules.

5|Oenothera rosea | 640 | 1/40 x 1/80 |Ovate.

6|Hypericum hirsutum | 700 | 1/30 x 1/100 |Cylindrical, rough.

7|Mimulus luteus | 2,900 | 1/60 x 1/100 |Oval, minute.

8|Penthorum sedoides | 8,000\* | 1/70 x 1/150 |Flattened, very minute.

9|Sagina procumbens | 12,000\* | 1/120 |Sub-triangular, flat.

10|Orchis maculata | 15,000\* | --- |Margined, flat,

| | | | very minute.

11|Gentiana purpurea | 35 | 1/25 |Wavy, rough, with this

| | | | coriaceous margins.

12|Silene alpina | --- | 1/30 |Flat, with fringed

| | | | margins.

13|Adenophora communis | --- | 1/20 x 1/40 |Very thin, wavy, light.

|Quartz grains | 25,000 | 1/250 |Deep sea ... 700 miles.

|Do. |200,000 | 1/500 |Genoa ... 600 miles.

If now we compare the seeds with the quartz grains, we find that

several are from twice to three times the weight of the grains found by

Mr. Murray, and others five times, eight times, and fifteen times as

heavy; but they are proportionately very much larger, and, being usually

irregular in shape or compressed, they expose a very much larger surface

to the air. The surface is often rough, and several have dilated margins

or tailed appendages, increasing friction and rendering the uniform rate

of falling through still air immensely less than in the case of the

smooth, rounded, solid quartz grains. With these advantages it is a

moderate estimate that seeds ten times the weight of the quartz grains

could be carried quite as far through the air by a violent gale and

under the most favourable conditions. These limits will include five of

the seeds here given, as well as hundreds of others which do not exceed

them in weight; and to these we may add some larger seeds which have

other favourable characteristics, as is the case with numbers 11-13,

which, though very much larger than the rest, are so formed as in all

probability to be still more easily carried great distances by a gale of

wind. It appears, therefore, to be absolutely certain that every

autumnal gale capable of conveying solid mineral particles to great

distances, must also carry numbers of small seeds at least as far; and

if this is so, the wind alone will form one of the most effective agents

in the dispersal of plants.

Hitherto this mode of conveyance, as applying to the transmission of

seeds for great distances across the ocean, has been rejected by

botanists, for two reasons. In the first place, there is said to be no

direct evidence of such conveyance; and, secondly, the peculiar plants

of remote oceanic islands do not appear to have seeds specially adapted

for aerial transmission. I will consider briefly each of these

objections.

\_Objection to the Theory of Wind-Dispersal.\_

To obtain direct evidence of the transmission of such minute and

perishable objects, which do not exist in great quantities, and are

probably carried to the greatest distances but rarely and as single

specimens, is extremely difficult. A bird or insect can be seen if it

comes on board ship, but who would ever detect the seeds of Mimulus or

Orchis even if a score of them fell on a ship's deck? Yet if but one

such seed per century were carried to an oceanic island, that island

might become rapidly overrun by the plant, if the conditions were

favourable to its growth and reproduction. It is further objected that

search has been made for such seeds, and they have not been found.

Professor Kerner of Innsbruck examined the snow on the surface of

glaciers, and assiduously collected all the seeds he could find, and

these were all of plants which grew in the adjacent mountains or in the

same district. In like manner, the plants growing on moraines were found

to be those of the adjacent mountains, plateaux, or lowlands. Hence he

concluded that the prevalent opinion that seeds may be carried through

the air for very great distances "is not supported by fact."[176] The

opinion is certainly not supported by Kerner's facts, but neither is it

opposed by them. It is obvious that the seeds that would be carried by

the wind to moraines or to the surface of glaciers would be, first and

in the greatest abundance, those of the immediately surrounding

district; then, very much more rarely, those from more remote mountains;

and lastly, in extreme rarity, those from distant countries or

altogether distinct mountain ranges. Let us suppose the first to be so

abundant that a single seed could be found by industrious search on each

square yard of the surface of the glacier; the second so scarce that

only one could possibly be found in a hundred yards square; while to

find one of the third class it would be necessary exhaustively to

examine a square mile of surface. Should we expect that \_one\_ ever to be

found, and should the fact that it could not be found be taken as a

proof that it was not there? Besides, a glacier is altogether in a bad

position to receive such remote wanderers, since it is generally

surrounded by lofty mountains, often range behind range, which would

intercept the few air-borne seeds that might have been carried from a

distant land. The conditions in an oceanic island, on the other hand,

are the most favourable, since the land, especially if high, will

intercept objects carried by the wind, and will thus cause more of the

solid matter to fall on it than on an equal area of ocean. We know that

winds at sea often blow violently for days together, and the rate of

motion is indicated by the fact that 72 miles an hour was the average

velocity of the wind observed during twelve hours at the Ben Nevis

observatory, while the velocity sometimes rises to 120 miles an hour. A

twelve hours' gale might, therefore, carry light seeds a thousand miles

as easily and certainly as it could carry quartz-grains of much greater

specific gravity, rotundity, and smoothness, 500 or even 100 miles; and

it is difficult even to imagine a sufficient reason why they should not

be so carried--perhaps very rarely and under exceptionally favourable

conditions,--but this is all that is required.

As regards the second objection, it has been observed that orchideae,

which have often exceedingly small and light seeds, are remarkably

absent from oceanic islands. This, however, may be very largely due to

their extreme specialisation and dependence on insect agency for their

fertilisation; while the fact that they do occur in such very remote

islands as the Azores, Tahiti, and the Sandwich Islands, proves that

they must have once reached these localities either by the agency of

birds or by transmission through the air; and the facts I have given

above render the latter mode at least as probable as the former. Sir

Joseph Hooker remarks on the composite plant of Kerguelen Island (Cotula

plumosa) being found also on Lord Auckland and MacQuarrie Islands, and

yet having no pappus, while other species of the genus possess it. This

is certainly remarkable, and proves that the plant must have, or once

have had, some other means of dispersal across wide oceans.[177] One of

the most widely dispersed species in the whole world (Sonchus oleraceus)

possesses pappus, as do four out of five of the species which are common

to Europe and New Zealand, all of which have a very wide distribution.

The same author remarks on the limited area occupied by most species of

Compositae, notwithstanding their facilities for dispersal by means of

their feathered seeds; but it has been already shown that limitations

of area are almost always due to the competition of allied forms,

facilities for dispersal being only one of many factors in determining

the wide range of species. It is, however, a specially important factor

in the case of the inhabitants of remote oceanic islands, since, whether

they are peculiar species or not, they or their remote ancestors must at

some time or other have reached their present position by natural means.

I have already shown elsewhere, that the flora of the Azores strikingly

supports the view of the species having been introduced by aerial

transmission only, that is, by the agency of birds and the wind, because

all plants that could not possibly have been carried by these means are

absent.[178] In the same way we may account for the extreme rarity of

Leguminosae in all oceanic islands. Mr. Hemsley, in his Report on

Insular Floras, says that they "are wanting in a large number of oceanic

islands where there is no true littoral flora," as St. Helena, Juan

Fernandez, and all the islands of the South Atlantic and South Indian

Oceans. Even in the tropical islands, such as Mauritius and Bourbon,

there are no endemic species, and very few in the Galapagos and the

remoter Pacific Islands. All these facts are quite in accordance with

the absence of facilities for transmission through the air, either by

birds or the wind, owing to the comparatively large size and weight of

the seeds; and an additional proof is thus afforded of the extreme

rarity of the successful floating of seeds for great distances across

the ocean.[179]

\_Explanation of North Temperate Plants in the Southern Hemisphere.\_

If we now admit that many seeds which are either minute in size, of thin

texture or wavy form, or so fringed or margined as to afford a good hold

to the air, are capable of being carried for many hundreds of miles by

exceptionally violent and long-continued gales of wind, we shall not

only be better able to account for the floras of some of the remotest

oceanic islands, but shall also find in the fact a sufficient

explanation of the wide diffusion of many genera, and even species, of

arctic and north temperate plants in the southern hemisphere or on the

summits of tropical mountains. Nearly fifty of the flowering plants of

Tierra-del-Fuego are found also in North America or Europe, but in no

intermediate country; while fifty-eight species are common to New

Zealand and Northern Europe; thirty-eight to Australia, Northern Europe,

and Asia; and no less than seventy-seven common to New Zealand,

Australia, and South America.[180] On lofty mountains far removed from

each other, identical or closely allied plants often occur. Thus the

fine Primula imperialis of a single mountain peak in Java has been found

(or a closely allied species) in the Himalayas; and many other plants of

the high mountains of Java, Ceylon, and North India are either identical

or closely allied forms. So, in Africa, some species, found on the

summits of the Cameroons and Fernando Po in West Africa, are closely

allied to species in the Abyssinian highlands and in Temperate Europe;

while other Abyssinian and Cameroons species have recently been found on

the mountains of Madagascar. Some peculiar Australian forms have been

found represented on the summit of Kini Balu in Borneo. Again, on the

summit of the Organ mountains in Brazil there are species allied to

those of the Andes, but not found in the intervening lowlands.

\_No Proof of Recent Lower Temperature in the Tropics.\_

Now all these facts, and numerous others of like character, were

supposed by Mr. Darwin to be due to a lowering of temperature during

glacial epochs, which allowed these temperate forms to migrate across

the intervening tropical lowlands. But any such change within the epoch

of existing species is almost inconceivable. In the first place, it

would necessitate the extinction of much of the tropical flora (and with

it of the insect life), because without such extinction alpine

herbaceous plants could certainly never spread over tropical forest

lowlands; and, in the next place, there is not a particle of direct

evidence that any such lowering of temperature in inter-tropical

lowlands ever took place. The only alleged evidence of the kind is that

adduced by the late Professor Agassiz and Mr. Hartt; but I am informed

by my friend, Mr. J.C. Branner (now State Geologist of Arkansas, U.S.),

who succeeded Mr. Hartt, and spent several years completing the

geological survey of Brazil, that the supposed moraines and glaciated

granite rocks near Rio Janeiro and elsewhere, as well as the so-called

boulder-clay of the same region, are entirely explicable as the results

of sub-aerial denudation and weathering, and that there is no proof

whatever of glaciation in any part of Brazil.

\_Lower Temperature not needed to Explain the Facts.\_

But any such vast physical change as that suggested by Darwin, involving

as it does such tremendous issues as regards its effects on the tropical

fauna and flora of the whole world, is really quite uncalled for,

because the facts to be explained are of the same essential nature as

those presented by remote oceanic islands, between which and the nearest

continents no temperate land connection is postulated. In proportion to

their limited area and extreme isolation, the Azores, St. Helena, the

Galapagos, and the Sandwich Islands, each possess a fairly rich--the

last a very rich--indigenous flora; and the means which sufficed to

stock them with a great variety of plants would probably suffice to

transmit others from mountain-top to mountain-top in various parts of

the globe. In the case of the Azores, we have large numbers of species

identical with those of Europe, and others closely allied, forming an

exactly parallel case to the species found on the various mountain

summits which have been referred to. The distances from Madagascar to

the South African mountains and to Kilimandjaro, and from the latter to

Abyssinia, are no greater than from Spain to the Azores, while there are

other equatorial mountains forming stepping-stones at about an equal

distance to the Cameroons. Between Java and the Himalayas we have the

lofty mountains of Sumatra and of North-western Burma, forming steps at

about the same distance apart; while between Kini Balu and the

Australian Alps we have the unexplored snow mountains of New Guinea,

the Bellenden Ker mountains in Queensland, and the New England and Blue

Mountains of New South Wales. Between Brazil and Bolivia the distances

are no greater; while the unbroken range of mountains from Arctic

America to Tierra-del-Fuego offers the greatest facilities for

transmission, the partial gap between the lofty peak of Chiriqui and the

high Andes of New Grenada being far less than from Spain to the Azores.

Thus, whatever means have sufficed for stocking oceanic islands must

have been to some extent effective in transmitting northern forms from

mountain to mountain, across the equator, to the southern hemisphere;

while for this latter form of dispersal there are special facilities, in

the abundance of fresh and unoccupied surfaces always occurring in

mountain regions, owing to avalanches, torrents, mountain-slides, and

rock-falls, thus affording stations on which air-borne seeds may

germinate and find a temporary home till driven out by the inroads of

the indigenous vegetation. These temporary stations may be at much lower

altitudes than the original habitat of the species, if other conditions

are favourable. Alpine plants often descend into the valleys on glacial

moraines, while some arctic species grow equally well on mountain

summits and on the seashore. The distances above referred to between the

loftier mountains may thus be greatly reduced by the occurrence of

suitable conditions at lower altitudes, and the facilities for

transmission by means of aerial currents proportionally increased.[181]

\_Facts Explained by the Wind-Carriage of Seeds.\_

But if we altogether reject aerial transmission of seeds for great

distances, except by the agency of birds, it will be difficult, if not

impossible, to account for the presence of so many identical species of

plants on remote mountain summits, or for that "continuous current of

vegetation" described by Sir Joseph Hooker as having apparently long

existed from the northern to the southern hemisphere. It may be admitted

that we can, possibly, account for the greater portion of the floras of

remote oceanic islands by the agency of birds alone; because, when blown

out to sea land-birds must reach some island or perish, and all which

come within sight of an island will struggle to reach it as their only

refuge. But, with mountain summits the case is altogether different,

because, being surrounded by land instead of by sea, no bird would need

to fly, or to be carried by the wind, for several hundred miles at a

stretch to another mountain summit, but would find a refuge in the

surrounding uplands, ridges, valleys, or plains. As a rule the birds

that frequent lofty mountain tops are peculiar species, allied to those

of the surrounding district; and there is no indication whatever of the

passage of birds from one remote mountain to another in any way

comparable with the flights of birds which are known to reach the Azores

annually, or even with the few regular migrants from Australia to New

Zealand. It is almost impossible to conceive that the seeds of the

Himalayan primula should have been thus carried to Java; but, by means

of gales of wind, and intermediate stations from fifty to a few hundred

miles apart, where the seeds might vegetate for a year or two and

produce fresh seed to be again carried on in the same manner, the

transmission might, after many failures, be at last effected.

A very important consideration is the vastly larger scale on which

wind-carriage of seeds must act, as compared with bird-carriage. It can

only be a few birds which carry seeds attached to their feathers or

feet. A very small proportion of these would carry the seeds of Alpine

plants; while an almost infinitesimal fraction of these latter would

convey the few seeds attached to them safely to an oceanic island or

remote mountain. But winds, in the form of whirlwinds or tornadoes,

gales or hurricanes, are perpetually at work over large areas of land

and sea. Insects and light particles of matter are often carried up to

the tops of high mountains; and, from the very nature and origin of

winds, they usually consist of ascending or descending currents, the

former capable of suspending such small and light objects as are many

seeds long enough for them to be carried enormous distances. For each

single seed carried away by external attachment to the feet or feathers

of a bird, countless millions are probably carried away by violent

winds; and the chance of conveyance to a great distance and in a

definite direction must be many times greater by the latter mode than

by the former.[182] We have seen that inorganic particles of much

greater specific gravity than seeds, and nearly as heavy as the smallest

kinds, are carried to great distances through the air, and we can

therefore hardly doubt that some seeds are carried as far. The direct

agency of the wind, as a supplement to bird-transport, will help to

explain the presence in oceanic islands of plants growing in dry or

rocky places whose small seeds are not likely to become attached to

birds; while it seems to be the only effective agency possible in the

dispersal of those species of alpine or sub-alpine plants found on the

summits of distant mountains, or still more widely separated in the

temperate zones of the northern and southern hemispheres.

\_Concluding Remarks.\_

On the general principles that have been now laid down, it will be found

that all the chief facts of the geographical distribution of animals and

plants can be sufficiently understood. There will, of course, be many

cases of difficulty and some seeming anomalies, but these can usually be

seen to depend on our ignorance of some of the essential factors of the

problem. Either we do not know the distribution of the group in recent

geological times, or we are still ignorant of the special methods by

which the organisms are able to cross the sea. The latter difficulty

applies especially to the lizard tribe, which are found in almost all

the tropical oceanic islands; but the particular mode in which they are

able to traverse a wide expanse of ocean, which is a perfect barrier to

batrachia and almost so to snakes, has not yet been discovered. Lizards

are found in all the larger Pacific Islands as far as Tahiti, while

snakes do not extend beyond the Fiji Islands; and the latter are also

absent from Mauritius and Bourbon, where lizards of seven or eight

species abound. Naturalists resident in the Pacific Islands would make a

valuable contribution to our science by studying the life-history of the

native lizards, and endeavouring to ascertain the special facilities

they possess for crossing over wide spaces of ocean.

FOOTNOTES:

[Footnote 163: See A. Agassiz, \_Three Cruises of the Blake\_ (Cambridge,

Mass., 1888), vol. i. p. 127, footnote.]

[Footnote 164: Even the extremely fine Mississippi mud is nowhere found

beyond a hundred miles from the mouths of the river in the Gulf of

Mexico (A. Agassiz, \_Three Cruises of the Blake\_, vol. i. p. 128).]

[Footnote 165: I have given a full summary of the evidence for the

permanence of oceanic and continental areas in my \_Island Life\_, chap.

vi.]

[Footnote 166: For a full account of the peculiarities of the Madagascar

fauna, see my \_Island Life\_, chap. xix.]

[Footnote 167: See \_Island Life\_, p. 446, and the whole of chaps. xxi.

xxii. More recent soundings have shown that the Map at p. 443, as well

as that of the Madagascar group at p. 387, are erroneous, the ocean

around Norfolk Island and in the Straits of Mozambique being more than

1000 fathoms deep. The general argument is, however, unaffected.]

[Footnote 168: For some details of these migrations, see the author's

\_Geographical Distribution of Animals\_, vol. i. p. 140; also Heilprin's

\_Geographical and Geological Distribution of Animals\_.]

[Footnote 169: For a full discussion of this question, see \_Island

Life\_, pp. 390-420.]

[Footnote 170: \_GÃ©ographie Botanique\_, p. 798.]

[Footnote 171: \_Nature\_, 1st April 1886.]

[Footnote 172: Report of the Brit. Assoc. Committee on Migration of

Birds during 1886.]

[Footnote 173: \_Trans. Ent. Soc.\_, 1871, p. 184.]

[Footnote 174: \_Nature\_ (1875), vol. xii. pp. 279, 298.]

[Footnote 175: I am indebted to Professor R. Meldola of the Finsbury

Technical Institute, and Rev. T.D. Titmas of Charterhouse for furnishing

me with the weights required.]

[Footnote 176: See \_Nature\_, vol. vi. p. 164, for a summary of Kerner's

paper.]

[Footnote 177: It seems quite possible that the absence of pappus in

this case is a recent adaptation, and that it has been brought about by

causes similar to those which have reduced or aborted the wings of

insects in oceanic islands. For when a plant has once reached one of the

storm-swept islands of the southern ocean, the pappus will be injurious

for the same reason that the wings of insects are injurious, since it

will lead to the seeds being blown out to sea and destroyed. The seeds

which are heaviest and have least pappus will have the best chance of

falling on the ground and remaining there to germinate, and this process

of selection might rapidly lead to the entire disappearance of the

pappus.]

[Footnote 178: See \_Island Life\_, p. 251.]

[Footnote 179: Mr. Hemsley suggests that it is not so much the

difficulty of transmission by floating, as the bad conditions the seeds

are usually exposed to when they reach land. Many, even if they

germinate, are destroyed by the waves, as Burchell noticed at St.

Helena; while even a flat and sheltered shore would be an unsuitable

position for many inland plants. Air-borne seeds, on the other hand, may

be carried far inland, and so scattered that some of them are likely to

reach suitable stations.]

[Footnote 180: For fuller particulars, see Sir J. Hooker's \_Introduction

to Floras of New Zealand and Australia\_, and a summary in my \_Island

Life\_, chaps. xxii. xxiii.]

[Footnote 181: For a fuller discussion of this subject, see my \_Island

Life\_, chap. xxiii.]

[Footnote 182: A very remarkable case of wind conveyance of seeds on a

large scale is described in a letter from Mr. Thomas Hanbury to his

brother, the late Daniel Hanbury, which has been kindly communicated to

me by Mr. Hemsley of Kew. The letter is dated "Shanghai, 1st May 1856,"

and the passage referred to is as follows:--

"For the past three days we have had very warm weather for this time of

year, in fact almost as warm as the middle of summer. Last evening the

wind suddenly changed round to the north and blew all night with

considerable violence, making a great change in the atmosphere.

"This morning, myriads of small white particles are floating about in

the air; there is not a single cloud and no mist, yet the sun is quite

obscured by this substance, and it looks like a white fog in England. I

enclose thee a sample, thinking it may interest. It is evidently a

vegetable production; I think, apparently, some kind of seed."

Mr. Hemsley adds, that this substance proves to be the plumose seeds of

a poplar or willow. In order to produce the effects described--\_quite

obscuring the sun like a white fog\_,--the seeds must have filled the air

to a very great height; and they must have been brought from some

district where there were extensive tracts covered with the tree which

produced them.]

CHAPTER XIII

THE GEOLOGICAL EVIDENCES OF EVOLUTION

What we may expect--The number of known species of extinct

animals--Causes of the imperfection of the geological

record--Geological evidences of

evolution--Shells--Crocodiles--The rhinoceros tribe--The

pedigree of the horse tribe--Development of deer's horns--Brain

development--Local relations of fossil and living animals--Cause

of extinction of large animals--Indications of general progress

in plants and animals--The progressive development of

plants--Possible cause of sudden late appearance of

exogens--Geological distribution of insects--Geological

succession of vertebrata--Concluding remarks.

The theory of evolution in the organic world necessarily implies that

the forms of animals and plants have, broadly speaking, progressed from

a more generalised to a more specialised structure, and from simpler to

more complex forms. We know, however, that this progression has been by

no means regular, but has been accompanied by repeated degradation and

degeneration; while extinction on an enormous scale has again and again

stopped all progress in certain directions, and has often compelled a

fresh start in development from some comparatively low and imperfect

type.

The enormous extension of geological research in recent times has made

us acquainted with a vast number of extinct organisms, so vast that in

some important groups--such as the mollusca--the fossil are more

numerous than the living species; while in the mammalia they are not

much less numerous, the preponderance of living species being chiefly in

the smaller and in the arboreal forms which have not been so well

preserved as the members of the larger groups. With such a wealth of

material to illustrate the successive stages through which animals have

passed, it will naturally be expected that we should find important

evidence of evolution. We should hope to learn the steps by which some

isolated forms have been connected with their nearest allies, and in

many cases to have the gaps filled up which now separate genus from

genus, or species from species. In some cases these expectations are

fulfilled, but in many other cases we seek in vain for evidence of the

kind we desire; and this absence of evidence with such an apparent

wealth of material is held by many persons to throw doubt on the theory

of evolution itself. They urge, with much appearance of reason, that all

the arguments we have hitherto adduced fall short of demonstration, and

that the crucial test consists in being able to show, in a great number

of cases, those connecting links which we say must have existed. Many of

the gaps that still remain are so vast that it seems incredible to these

writers that they could ever have been filled up by a close succession

of species, since these must have spread over so many ages, and have

existed in such numbers, that it seems impossible to account for their

total absence from deposits in which great numbers of species belonging

to other groups are preserved and have been discovered. In order to

appreciate the force, or weakness, of these objections, we must inquire

into the character and completeness of that record of the past life of

the earth which geology has unfolded, and ascertain the nature and

amount of the evidence which, under actual conditions, we may expect to

find.

\_The Number of known Species of Extinct Animals.\_

When we state that the known fossil mollusca are considerably more

numerous than those which now live on the earth, it appears at first

sight that our knowledge is very complete, but this is far from being

the case. The species have been continually changing throughout

geological time, and at each period have probably been as numerous as

they are now. If we divide the fossiliferous strata into twelve great

divisions--the Pliocene, Miocene, Eocene, Cretaceous, Oolite, Lias,

Trias, Permian, Carboniferous, Devonian, Silurian, and Cambrian,--we

find not only that each has a very distinct and characteristic molluscan

fauna, but that the different subdivisions often present a widely

different series of species; so that although a certain number of

species are common to two or more of the great divisions, the totality

of the species that have lived upon the earth must be very much more

than twelve times--perhaps even thirty or forty times--the number now

living. In like manner, although the species of fossil mammals now

recognised by more or less fragmentary fossil remains may not be much

less numerous than the living species, yet the duration of existence of

these was comparatively so short that they were almost completely

changed, perhaps six or seven times, during the Tertiary period; and

this is certainly only a fragment of the geological time during which

mammalia existed on the globe.

There is also reason to believe that the higher animals were much more

abundant in species during past geological epochs than now, owing to the

greater equability of the climate which rendered even the arctic regions

as habitable as the temperate zones are in our time.

The same equable climate would probably cause a more uniform

distribution of moisture, and render what are now desert regions capable

of supporting abundance of animal life. This is indicated by the number

and variety of the species of large animals that have been found fossil

in very limited areas which they evidently inhabited at one period. M.

Albert Gaudry found, in the deposits of a mountain stream at Pikermi in

Greece, an abundance of large mammalia such as are nowhere to be found

living together at the present time. Among them were two species of

Mastodon, two different rhinoceroses, a gigantic wild boar, a camel and

a giraffe larger than those now living, several monkeys, carnivora

ranging from martens and civets to lions and hyaenas of the largest

size, numerous antelopes of at least five distinct genera, and besides

these many forms altogether extinct. Such were the great herds of

Hipparion, an ancestral form of horse; the Helladotherium, a huge animal

bigger than the giraffe; the Ancylotherium, one of the Edentata; the

huge Dinotherium; the Aceratherium, allied to the rhinoceros; and the

monstrous Chalicotherium, allied to the swine and ruminants, but as

large as a rhinoceros; and to prey upon these, the great Machairodus or

sabre-toothed tiger. And all these remains were found in a space 300

paces long by 60 paces broad, many of the species existing in enormous

quantities.

The Pikermi fossils belong to the Upper Miocene formation, but an

equally rich deposit of Upper Eocene age has been discovered in

South-Western France at Quercy, where M. Filhol has determined the

presence of no less than forty-two species of beasts of prey alone.

Equally remarkable are the various discoveries of mammalian fossils in

North America, especially in the old lake bottoms now forming what are

called the "bad lands" of Dakota and Nebraska, belonging to the Miocene

period. Here are found an enormous assemblage of remains, often perfect

skeletons, of herbivora and carnivora, as varied and interesting as

those from the localities already referred to in Europe; but altogether

distinct, and far exceeding, in number and variety of species of the

larger animals, the whole existing fauna of North America. Very similar

phenomena occur in South America and in Australia, leading us to the

conclusion that the earth at the present time is impoverished as regards

the larger animals, and that at each successive period of Tertiary time,

at all events, it contained a far greater number of species than now

inhabit it. The very richness and abundance of the remains which we find

in limited areas, serve to convince us how imperfect and fragmentary

must be our knowledge of the earth's fauna at any one past epoch; since

we cannot believe that all, or nearly all, of the animals which

inhabited any district were entombed in a single lake, or overwhelmed by

the floods of a single river.

But the spots where such rich deposits occur are exceedingly few and far

between when compared with the vast areas of continental land, and we

have every reason to believe that in past ages, as now, numbers of

curious species were rare or local, the commoner and more abundant

species giving a very imperfect idea of the existing series of animal

forms. Yet more important, as showing the imperfection of our knowledge,

is the enormous lapse of time between the several formations in which we

find organic remains in any abundance, so vast that in many cases we

find ourselves almost in a new world, all the species and most of the

genera of the higher animals having undergone a complete change.

\_Causes of the Imperfection of the Geological Record.\_

These facts are quite in accordance with the conclusions of geologists

as to the necessary imperfection of the geological record, since it

requires the concurrence of a number of favourable conditions to

preserve any adequate representation of the life of a given epoch. In

the first place, the animals to be preserved must not die a natural

death by disease, or old age, or by being the prey of other animals, but

must be destroyed by some accident which shall lead to their being

embedded in the soil. They must be either carried away by floods, sink

into bogs or quicksands, or be enveloped in the mud or ashes of a

volcanic eruption; and when thus embedded they must remain undisturbed

amid all the future changes of the earth's surface.

But the chances against this are enormous, because denudation is always

going on, and the rocks we now find at the earth's surface are only a

small fragment of those which were originally laid down. The

alternations of marine and freshwater deposits, and the frequent

unconformability of strata with those which overlie them, tell us

plainly of repeated elevations and depressions of the surface, and of

denudation on an enormous scale. Almost every mountain range, with its

peaks, ridges, and valleys, is but the remnant of some vast plateau

eaten away by sub-aerial agencies; every range of sea-cliffs tell us of

long slopes of land destroyed by the waves; while almost all the older

rocks which now form the surface of the earth have been once covered

with newer deposits which have long since disappeared. Nowhere are the

evidences of this denudation more apparent than in North and South

America, where granitic or metamorphic rocks cover an area hardly less

than that of all Europe. The same rocks are largely developed in Central

Africa and Eastern Asia; while, besides those portions that appear

exposed on the surface, areas of unknown extent are buried under strata

which rest on them uncomformably, and could not, therefore, constitute

the original capping under which the whole of these rocks must once have

been deeply buried; because granite can only be formed, and metamorphism

can only go on, deep down in the crust of the earth. What an

overwhelming idea does this give us of the destruction of whole piles

of rock, miles in thickness and covering areas comparable with those of

continents; and how great must have been the loss of the innumerable

fossil forms which those rocks contained! In view of such destruction we

are forced to conclude that our palaeontological collections, rich

though they may appear, are really but small and random samples, giving

no adequate idea of the mighty series of organism which have lived upon

the earth.[183]

Admitting, however, the extreme imperfection of the geological record as

a whole, it may be urged that certain limited portions of it are fairly

complete--as, for example, the various Miocene deposits of India,

Europe, and North America,--and that in these we ought to find many

examples of species and genera linked together by intermediate forms. It

may be replied that in several cases this really occurs; and the reason

why it does not occur more often is, that the theory of evolution

requires that distinct genera should be linked together, not by a direct

passage, but by the descent of both from a common ancestor, which may

have lived in some much earlier age the record of which is either

wanting or very incomplete. An illustration given by Mr. Darwin will

make this more clear to those who have not studied the subject. The

fantail and pouter pigeons are two very distinct and unlike breeds,

which we yet know to have been both derived from the common wild

rock-pigeon. Now, if we had every variety of living pigeon before us, or

even all those which have lived during the present century, we should

find no intermediate types between these two--none combining in any

degree the characters of the pouter with that of the fantail. Neither

should we ever find such an intermediate form, even had there been

preserved a specimen of every breed of pigeon since the ancestral

rock-pigeon was first tamed by man--a period of probably several

thousand years. We thus see that a complete passage from one very

distinct species to another could not be expected even had we a complete

record of the life of any one period. What we require is a complete

record of all the species that have existed since the two forms began

to diverge from their common ancestor, and this the known imperfection

of the record renders it almost impossible that we should ever attain.

All that we have a right to expect is, that, as we multiply the fossil

forms in any group, the gaps that at first existed in that group shall

become less wide and less numerous; and also that, in some cases, a

tolerably direct series shall be found, by which the more specialised

forms of the present day shall be connected with more generalised

ancestral types. We might also expect that when a country is now

characterised by special groups of animals, the fossil forms that

immediately preceded them shall, for the most part, belong to the same

groups; and further, that, comparing the more ancient with the more

modern types, we should find indications of progression, the earlier

forms being, on the whole, lower in organisation, and less specialised

in structure than the later. Now evidence of evolution of these varied

kinds is what we do find, and almost every fresh discovery adds to their

number and cogency. In order, therefore, to show that the testimony

given by geology is entirely in favour of the theory of descent with

modification, some of the more striking of the facts will now be given.

\_Geological Evidences of Evolution.\_

In an article in \_Nature\_ (vol. xiv. p. 275), Professor Judd calls

attention to some recent discoveries in the Hungarian plains, of fossil

lacustrine shells, and their careful study by Dr. Neumayr and M. Paul of

the Austrian Geological Survey. The beds in which they occur have

accumulated to the thickness of 2000 feet, containing throughout

abundance of fossils, and divisible into eight zones, each of which

exhibits a well-marked and characteristic fauna. Professor Judd then

describes the bearing of these discoveries as follows--

"The group of shells which affords the most interesting evidence

of the origin of new forms through descent with modification is

that of the genus Vivipara or Paludina, which occurs in

prodigious abundance throughout the whole series of freshwater

strata. We shall not, of course, attempt in this place to enter

into any details concerning the forty distinct \_forms\_ of this

genus (Dr. Neumayr very properly hesitates to call them all

\_species\_), which are named and described in this monograph,

and between which, as the authors show, so many connecting

links, clearly illustrating the derivation of the newer from the

older types, have been detected. On the minds of those who

carefully examine the admirably engraved figures given in the

plates accompanying this valuable memoir, or still better, the

very large series of specimens from among which the subjects of

these figures are selected, and which are now in the museum of

the Reichsanstalt of Vienna, but little doubt will, we suspect,

remain that the authors have fully made out their case, and have

demonstrated that, beyond all controversy, the series with

highly complicated ornamentation were variously derived by

descent--the lines of which are in most cases perfectly clear

and obvious--from the simple and unornamented Vivipara

achatinoides of the Congerien-Schichten (the lower division of

the series of strata). It is interesting to notice that a large

portion of these unquestionably derived forms depart so widely

from the type of the genus Vivipara, that they have been

separated on so high an authority as that of Sandberger, as a

new genus, under the name of Tulotoma. And hence we are led to

the conclusion that a vast number of forms, certainly exhibiting

specific distinctions, and according to some naturalists,

differences even entitled to be regarded of generic value, have

all a common ancestry."

It is, as Professor Judd remarks, owing to the exceptionally favourable

circumstances of a long-continued and unbroken series of deposits being

formed under physical conditions either identical or very slowly

changing, that we owe so complete a record of the process of organic

change. Usually, some disturbing elements, such as a sudden change of

physical conditions, or the immigration of new sets of forms from other

areas and the consequent retreat or partial extinction of the older

fauna, interferes with the continuity of organic development, and

produces those puzzling discordances so generally met with in geological

formations of marine origin. While a case of the kind now described

affords evidence of the origin of species complete and conclusive,

though on a necessarily very limited scale, the very rarity of the

conditions which are essential to such completeness serves to explain

why it is that in most cases the direct evidence of evolution is not to

be obtained.

Another illustration of the filling up of gaps between existing groups

is afforded by Professor Huxley's researches on fossil crocodiles. The

gap between the existing crocodiles and the lizards is very wide, but as

we go back in geological time we meet with fossil forms which are to

some extent intermediate and form a connected series. The three living

genera--Crocodilus, Alligator, and Gavialis--are found in the Eocene

formation, and allied forms of another genus, Holops, in the Chalk. From

the Chalk backward to the Lias another group of genera occurs, having

anatomical characteristics intermediate between the living crocodiles

and the most ancient forms. These, forming two genera Belodon and

Stagonolepis, are found in a still older formation, the Trias. They have

characters resembling some lizards, especially the remarkable Hatteria

of New Zealand, and have also some resemblances to the

Dinosaurians--reptiles which in some respects approach birds.

Considering how comparatively few are the remains of this group of

animals, the evidence which it affords of progressive development is

remarkably clear.[184]

Among the higher animals the rhinoceros, the horse, and the deer afford

good evidence of advance in organisation and of the filling up of the

gaps which separate the living forms from their nearest allies. The

earliest ancestral forms of the rhinoceroses occur in the Middle Eocene

of the United States, and were to some extent intermediate between the

rhinoceros and tapir families, having like the latter four toes to the

front feet, and three to those behind. These are followed in the Upper

Eocene by the genus Amynodon, in which the skull assumes more distinctly

the rhinocerotic type. Following this in the Lower Miocene we have the

Aceratherium, like the last in its feet, but still more decidedly a

rhinoceros in its general structure. From this there are two diverging

lines--one in the Old World, the other in the New. In the former, to

which the Aceratherium is supposed to have migrated in early Miocene

times, when a mild climate and luxuriant vegetation prevailed far within

the arctic circle, it gave rise to the Ceratorhinus and the various

horned rhinoceroses of late Tertiary times and of those now living. In

America a number of large hornless rhinoceroses were developed--they

are found in the Upper Miocene, Pliocene, and Post-Pliocene

formations--and then became extinct. The true rhinoceroses have three

toes on all the feet.[185]

\_The Pedigree of the Horse Tribe.\_

Yet more remarkable is the evidence afforded by the ancestral forms of

the horse tribe which have been discovered in the American tertiaries.

The family Equidae, comprising the living horse, asses, and zebras,

differ widely from all other mammals in the peculiar structure of the

feet, all of which terminate in a single large toe forming the hoof.

They have forty teeth, the molars being formed of hard and soft material

in crescentic folds, so as to be a powerful agent in grinding up hard

grasses and other vegetable food. The former peculiarities depend upon

modifications of the skeleton, which have been thus described by

Professor Huxley:--

"Let us turn in the first place to the fore-limb. In most

quadrupeds, as in ourselves, the fore-arm contains distinct

bones, called the radius and the ulna. The corresponding region

in the horse seems at first to possess but one bone. Careful

observation, however, enables us to distinguish in this bone a

part which clearly answers to the upper end of the ulna. This is

closely united with the chief mass of the bone which represents

the radius, and runs out into a slender shaft, which may be

traced for some distance downwards upon the back of the radius,

and then in most cases thins out and vanishes. It takes still

more trouble to make sure of what is nevertheless the fact, that

a small part of the lower end of the bone of a horse's fore-arm,

which is only distinct in a very young foal, is really the lower

extremity of the ulna.

"What is commonly called the knee of a horse is its wrist. The

'cannon bone' answers to the middle bone of the five metacarpal

bones which support the palm of the hand in ourselves. The

pastern, coronary, and coffin bones of veterinarians answer to

the joints of our middle fingers, while the hoof is simply a

greatly enlarged and thickened nail. But if what lies below the

horse's 'knee' thus corresponds to the middle finger in

ourselves, what has become of the four other fingers or digits?

We find in the places of the second and fourth digits only two

slender splintlike bones, about two-thirds as long as the cannon

bone, which gradually taper to their lower ends and bear no

finger joints, or, as they are termed, phalanges. Sometimes,

small bony or gristly nodules are to be found at the bases of

these two metacarpal splints, and it is probable that these

represent rudiments of the first and fifth toes. Thus, the part

of the horse's skeleton which corresponds with that of the human

hand, contains one overgrown middle digit, and at least two

imperfect lateral digits; and these answer, respectively, to the

third, the second, and the fourth fingers in man.

"Corresponding modifications are found in the hind limb. In

ourselves, and in most quadrupeds, the leg contains two distinct

bones, a large bone, the tibia, and a smaller and more slender

bone, the fibula. But, in the horse, the fibula seems, at first,

to be reduced to its upper end; a short slender bone united with

the tibia, and ending in a point below, occupying its place.

Examination of the lower end of a young foal's shin-bone,

however, shows a distinct portion of osseous matter which is the

lower end of the fibula; so that the, apparently single, lower

end of the shin-bone is really made up of the coalesced ends of

the tibia and fibula, just as the, apparently single, lower end

of the fore-arm bone is composed of the coalesced radius and

ulna.

"The heel of the horse is the part commonly known as the hock.

The hinder cannon bone answers to the middle metatarsal bone of

the human foot, the pastern, coronary, and coffin bones, to the

middle toe bones; the hind hoof to the nail; as in the forefoot.

And, as in the forefoot, there are merely two splints to

represent the second and the fourth toes. Sometimes a rudiment

of a fifth toe appears to be traceable.

"The teeth of a horse are not less peculiar than its limbs. The

living engine, like all others, must be well stoked if it is to

do its work; and the horse, if it is to make good its wear and

tear, and to exert the enormous amount of force required for its

propulsion, must be well and rapidly fed. To this end, good

cutting instruments and powerful and lasting crushers are

needful. Accordingly, the twelve cutting teeth of a horse are

close-set and concentrated in the forepart of its mouth, like so

many adzes or chisels. The grinders or molars are large, and

have an extremely complicated structure, being composed of a

number of different substances of unequal hardness. The

consequence of this is that they wear away at different rates;

and, hence, the surface of each grinder is always as uneven as

that of a good millstone."[186]

We thus see that the Equidae differ very widely in structure from most

other mammals. Assuming the truth of the theory of evolution, we should

expect to find traces among extinct animals of the steps by which this

great modification has been effected; and we do really find traces of

these steps, imperfectly among European fossils, but far more completely

among those of America.

It is a singular fact that, although no horse inhabited America when

discovered by Europeans, yet abundance of remains of extinct horses have

been found both in North and South America in Post-Tertiary and Upper

Pliocene deposits; and from these an almost continuous series of

modified forms can be traced in the Tertiary formation, till we reach,

at the very base of the series, a primitive form so unlike our perfected

animal, that, had we not the intermediate links, few persons would

believe that the one was the ancestor of the other. The tracing out of

this marvellous history we owe chiefly to Professor Marsh of Yale

College, who has himself discovered no less than thirty species of

fossil Equidae; and we will allow him to tell the story of the

development of the horse from a humble progenitor in his own words.

"The oldest representative of the horse at present known is the

diminutive Eohippus from the Lower Eocene. Several species have

been found, all about the size of a fox. Like most of the early

mammals, these ungulates had forty-four teeth, the molars with

short crowns and quite distinct in form from the premolars. The

ulna and fibula were entire and distinct, and there were four

well-developed toes and a rudiment of another on the forefeet,

and three toes behind. In the structure of the feet and teeth,

the Eohippus unmistakably indicates that the direct ancestral

line to the modern horse has already separated from the other

perissodactyles, or odd-toed ungulates.

"In the next higher division of the Eocene another genus,

Orohippus, makes its appearance, replacing Eohippus, and showing

a greater, though still distant, resemblance to the equine type.

The rudimentary first digit of the forefoot has disappeared, and

the last premolar has gone over to the molar series. Orohippus

was but little larger than Eohippus, and in most other respects

very similar. Several species have been found, but none occur

later than the Upper Eocene.

"Near the base of the Miocene, we find a third closely allied

genus, Mesohippus, which is about as large as a sheep, and one

stage nearer the horse. There are only three toes and a

rudimentary splint on the forefeet, and three toes behind. Two

of the premolar teeth are quite like the molars. The ulna is no

longer distinct or the fibula entire, and other characters show

clearly that the transition is advancing.

"In the Upper Miocene Mesohippus is not found, but in its place

a fourth form, Miohippus, continues the line. This genus is near

the Anchitherium of Europe, but presents several important

differences. The three toes in each foot are more nearly of a

size, and a rudiment of the fifth metacarpal bone is retained.

All the known species of this genus are larger than those of

Mesohippus, and none of them pass above the Miocene formation.

"The genus Protohippus of the Lower Pliocene is yet more equine,

and some of its species equalled the ass in size. There are

still three toes on each foot, but only the middle one,

corresponding to the single toe of the horse, comes to the

ground. This genus resembles most nearly the Hipparion of

Europe.

"In the Pliocene we have the last stage of the series before

reaching the horse, in the genus Pliohippus, which has lost the

small hooflets, and in other respects is very equine. Only in

the Upper Pliocene does the true Equus appear and complete the

genealogy of the horse, which in the Post-Tertiary roamed over

the whole of North and South America, and soon after became

extinct. This occurred long before the discovery of the

continent by Europeans, and no satisfactory reason for the

extinction has yet been given. Besides the characters I have

mentioned, there are many others in the skeleton, skull, teeth,

and brain of the forty or more intermediate species, which show

that the transition from the Eocene Eohippus to the modern Equus

has taken place in the order indicated"[187] (see Fig. 33).

[Illustration: FIG. 33.--Geological development of the horse tribe

(Eohippus since discovered).]

Well may Professor Huxley say that this is demonstrative evidence of

evolution; the doctrine resting upon exactly as secure a foundation as

did the Copernican theory of the motions of the heavenly bodies at the

time of its promulgation. Both have the same basis--the coincidence of

the observed facts with the theoretical requirements.

\_Development of Deer's Horns.\_

Another clear and unmistakable proof of evolution is afforded by one of

the highest and latest developed tribes of mammals--the true deer. These

differ from all other ruminants in possessing solid deciduous horns

which are always more or less branched. They first appear in the Middle

Miocene formation, and continue down to our time; and their development

has been carefully traced by Professor Boyd Dawkins, who thus summarises

his results:--

"In the middle stage of the Miocene the cervine antler consists

merely of a simple forked crown (as in Cervus dicroceros), which

increases in size in the Upper Miocene, although it still

remains small and erect, like that of the roe. In Cervus

Matheroni it measures 11Â·4 inches, and throws off not more than

four tines, all small. The deer living in Auvergne in the

succeeding or Pliocene age, present us with another stage in the

history of antler development. There, for the first time, we see

antlers of the Axis and Rusa type, larger and longer, and more

branching than any antlers were before, and possessing three or

more well-developed tines. Deer of this type abounded in

Pliocene Europe. They belong to the Oriental division of the

Cervidae, and their presence in Europe confirms the evidence of

the flora, brought forward by the Comte de Saporta, that the

Pliocene climate was warm. They have probably disappeared from

Europe in consequence of the lowering of the temperature in the

Pleistocene age, while their descendants have found a congenial

home in the warmer regions of Eastern Asia.

"In the latest stage of the Pliocene--the Upper Pliocene of the

Val d'Arno--the Cervus dicranios of Nesti presents us with

antlers much smaller than those of the Irish elk, but very

complicated in their branching. This animal survived into the

succeeding age, and is found in the pre-glacial forest bed of

Norfolk, being described by Dr. Falconer under the name of

Sedgwick's deer. The Irish elk, moose, stag, reindeer, and

fallow deer appear in Europe in the Pleistocene age, all with

highly complicated antlers in the adult, and the first

possessing the largest antlers yet known. Of these the Irish elk

disappeared in the Prehistoric age, after having lived in

countless herds in Ireland, while the rest have lived on into

our own times in Euro-Asia, and, with the exception of the last,

also in North America.

"From this survey it is obvious that the cervine antlers have

increased in size and complexity from the Mid-Miocene to the

Pleistocene age, and that their successive changes are analogous

to those which are observed in the development of antlers in the

living deer, which begin with a simple point, and increase in

number of tines till their limit of growth be reached. In other

words, the development of antlers indicated at successive and

widely-separated pages of the geological record is the same as

that observed in the history of a single living species. It is

also obvious that the progressive diminution of size and

complexity in the antlers, from the present time back into the

early Tertiary age, shows that we are approaching the zero of

antler development in the Mid-Miocene. No trace of any

antler-bearing ruminant has been met with in the lower Miocenes,

either of Europe or the United States."[188]

\_Progressive Brain-Development.\_

The three illustrations now given sufficiently prove that, whenever the

geological record approaches to completeness, we have evidence of the

progressive change of species in definite directions, and from less

developed to more developed types--exactly such a change as we may

expect to find if the evolution theory be the true one. Many other

illustrations of a similar change could be given, but the animal groups

in which they occur being less familiar, the details would be less

interesting, and perhaps hardly intelligible. There is, however, one

very remarkable proof of development that must be briefly noticed--that

afforded by the steady increase in the size of the brain. This may be

best stated in the words of Professor Marsh:--

"The real progress of mammalian life in America, from the

beginning of the Tertiary to the present, is well illustrated by

the brain-growth, in which we have the key to many other

changes. The earliest known Tertiary mammals all had very small

brains, and in some forms this organ was proportionally less

than in certain reptiles. There was a gradual increase in the

size of the brain during this period, and it is interesting to

find that this growth was mainly confined to the cerebral

hemispheres, or higher portion of the brain. In most groups of

mammals the brain has gradually become more convoluted, and thus

increased in quality as well as quantity. In some also the

cerebellum and olfactory lobes, the lower parts of the brain,

have even diminished in size. In the long struggle for existence

during Tertiary time the big brains won, then as now; and the

increasing power thus gained rendered useless many structures

inherited from primitive ancestors, but no longer adapted to new

conditions."

This remarkable proof of development in the organ of the mental

faculties, forms a fitting climax to the evidence already adduced of the

progressive evolution of the general structure of the body, as

illustrated by the bony skeleton. We now pass on to another class of

facts equally suggestive of evolution.

\_The Local Relations of Fossil and Living Animals.\_

If all existing animals have been produced from ancestral forms--mostly

extinct--under the law of variation and natural selection, we may expect

to find in most cases a close relation between the living forms of each

country and those which inhabited it in the immediately preceding epoch.

But if species have originated in some quite different way, either by

any kind of special creation, or by sudden advances of organisation in

the offspring of preceding types, such close relationship would not be

found; and facts of this kind become, therefore, to some extent a test

of evolution under natural selection or some other law of gradual

change. Of course the relationship will not appear when extensive

migration has occurred, by which the inhabitants of one region have been

able to take possession of another region, and destroy or drive out its

original inhabitants, as has sometimes happened. But such cases are

comparatively rare, except where great changes of climate are known to

have occurred; and we usually do find a remarkable continuity between

the existing fauna and flora of a country and those of the immediately

preceding age. A few of the more remarkable of these cases will now be

briefly noticed.

The mammalian fauna of Australia consists, as is well known, wholly of

the lowest forms--the Marsupials and Monotremata--except only a few

species of mice. This is accounted for by the complete isolation of the

country from the Asiatic continent during the whole period of the

development of the higher animals. At some earlier epoch the ancestral

marsupials, which abounded both in Europe and North America in the

middle of the Secondary period, entered the country, and have since

remained there, free from the competition of higher forms, and have

undergone a special development in accordance with the peculiar

conditions of a limited area. While in the large continents higher forms

of mammalia have been developed, which have almost or wholly

exterminated the less perfect marsupials, in Australia these latter have

become modified into such varied forms as the leaping kangaroos, the

burrowing wombats, the arboreal phalangers, the insectivorous

bandicoots, and the carnivorous Dasyuridae or native cats, culminating

in the Thylacinus or "tiger-wolf" of Tasmania--animals as unlike each

other as our sheep, rabbits, squirrels, and dogs, but all retaining the

characteristic features of the marsupial type.

Now in the caves and late Tertiary or Post-Tertiary deposits of

Australia the remains of many extinct mammalia have been found, but all

are marsupials. There are many kangaroos, some larger than any living

species, and others more allied to the tree-kangaroos of New Guinea; a

large wombat as large as a tapir; the Diprotodon, a thick-limbed

kangaroo the size of a rhinoceros or small elephant; and a quite

different animal, the Nototherium, nearly as large. The carnivorous

Thylacinus of Tasmania is also found fossil; and a huge phalanger,

Thylacoleo, the size of a lion, believed by Professor Owen and by

Professor Oscar Schmidt to have been equally carnivorous and

destructive.[189] Besides these, there are many other species more

resembling the living forms both in size and structure, of which they

may be, in some cases, the direct ancestors. Two species of extinct

Echidna, belonging to the very low Monotremata, have also been found in

New South Wales.

Next to Australia, South America possesses the most remarkable

assemblage of peculiar mammals, in its numerous Edentata--the sloths,

ant-eaters, and armadillos; its rodents, such as the cavies and

chinchillas; its marsupial opossums, and its quadrumana of the family

Cebidae. Remains of extinct species of all these have been found in the

caves of Brazil, of Post-Pliocene age; while in the earlier Pliocene

deposits of the pampas many distinct genera of these groups have been

found, some of gigantic size and extraordinary form. There are

armadillos of many types, some being as large as elephants; gigantic

sloths of the genera Megatherium, Megalonyx, Mylodon, Lestodon, and many

others; rodents belonging to the American families Cavidae and

Chinchillidae; and ungulates allied to the llama; besides many other

extinct forms of intermediate types or of uncertain affinities.[190] The

extinct Moas of New Zealand--huge wingless birds allied to the living

Apteryx--illustrate the same general law.

The examples now quoted, besides illustrating and enforcing the general

fact of evolution, throw some light on the usual character of the

modification and progression of animal forms. In the cases where the

geological record is tolerably complete, we find a continuous

development of some kind--either in complexity of ornamentation, as in

the fossil Paludinas of the Hungarian lake-basins; in size and in the

specialisation of the feet and teeth, as in the American fossil horses;

or in the increased development of the branching horns, as in the true

deer. In each of these cases specialisation and adaptation to the

conditions of the environment appear to have reached their limits, and

any change of these conditions, especially if it be at all rapid or

accompanied by the competition of less developed but more adaptable

forms, is liable to cause the extinction of the most highly developed

groups. Such we know was the case with the horse tribe in America, which

totally disappeared in that continent at an epoch so recent that we

cannot be sure that the disappearance was not witnessed, perhaps caused,

by man; while even in the Eastern hemisphere it is the smaller

species--the asses and the zebras--that have persisted, while the larger

and more highly developed true horses have almost, if not quite,

disappeared in a state of nature. So we find, both in Australia and

South America, that in a quite recent period many of the largest and

most specialised forms have become extinct, while only the smaller types

have survived to our day; and a similar fact is to be observed in many

of the earlier geological epochs, a group progressing and reaching a

maximum of size or complexity and then dying out, or leaving at most but

few and pigmy representatives.

\_Cause of Extinction of Large Animals.\_

Now there are several reasons for the repeated extinction of large

rather than of small animals. In the first place, animals of great bulk

require a proportionate supply of food, and any adverse change of

conditions would affect them more seriously than it would smaller

animals. In the next place, the extreme specialisation of many of these

large animals would render it less easy for them to be modified in any

new direction suited to changed conditions. Still more important,

perhaps, is the fact that very large animals always increase slowly as

compared with small ones--the elephant producing a single young one

every three years, while a rabbit may have a litter of seven or eight

young two or three times a year. Now the probability of favourable

variations will be in direct proportion to the population of the

species, and as the smaller animals are not only many hundred times more

numerous than the largest, but also increase perhaps a hundred times as

rapidly, they are able to become quickly modified by variation and

natural selection in harmony with changed conditions, while the large

and bulky species, being unable to vary quickly enough, are obliged to

succumb in the struggle for existence. As Professor Marsh well observes:

"In every vigorous primitive type which was destined to survive many

geological changes, there seems to have been a tendency to throw off

lateral branches, which became highly specialised and soon died out,

because they were unable to adapt themselves to new conditions." And he

goes on to show how the whole narrow path of the persistent Suilline

type, throughout the entire series of the American tertiaries, is

strewed with the remains of such ambitious offshoots, many of them

attaining the size of a rhinoceros; "while the typical pig, with an

obstinacy never lost, has held on in spite of catastrophes and

evolution, and still lives in America to-day."

\_Indications of General Progression in Plants and Animals.\_

One of the most powerful arguments formerly adduced against evolution

was, that geology afforded no evidence of the gradual development of

organic forms, but that whole tribes and classes appeared suddenly at

definite epochs, and often in great variety and exhibiting a very

perfect organisation. The mammalia, for example, were long thought to

have first appeared in Tertiary times, where they are represented in

some of the earlier deposits by all the great divisions of the class

fully developed--carnivora, rodents, insectivora, marsupials, and even

the perissodactyle and artiodactyle divisions of the ungulata--as

clearly defined as at the present day. The discovery in 1818 of a single

lower jaw in the Stonesfield Slate of Oxfordshire hardly threw doubt on

the generalisation, since either its mammalian character was denied, or

the geological position of the strata, in which it was found, was held

to have been erroneously determined. But since then, at intervals of

many years, other remains of mammalia have been discovered in the

Secondary strata, ranging from the Upper Oolite to the Upper Trias both

in Europe and the United States, and one even (Tritylodon) in the Trias

of South Africa. All these are either marsupials, or of some still lower

type of mammalia; but they consist of many distinct forms classed in

about twenty genera. Nevertheless, a great gap still exists between

these mammals and those of the Tertiary strata, since no mammal of any

kind has been found in any part of the Cretaceous formation, although in

several of its subdivisions abundance of land plants, freshwater shells,

and air-breathing reptiles have been discovered. So with fishes. In the

last century none had been obtained lower than the Carboniferous

formation; thirty years later they were found to be very abundant in the

Devonian rocks, and later still they were discovered in the Upper Ludlow

and Lower Ludlow beds of the Silurian formation.

We thus see that such sudden appearances are deceptive, and are, in

fact, only what we ought to expect from the known imperfection of the

geological record. The conditions favourable to the fossilisation of any

group of animals occur comparatively rarely, and only in very limited

areas; while the conditions essential for their permanent preservation

in the rocks, amid all the destruction caused by denudation or

metamorphism, are still more exceptional. And when they are thus

preserved to our day, the particular part of the rocks in which they lie

hidden may not be on the surface but buried down deep under other

strata, and may thus, except in the case of mineral-bearing deposits, be

altogether out of our reach. Then, again, how large a proportion of the

earth consists of wild and uncivilised regions in which no exploration

of the rocks has been yet made, so that whether we shall find the

fossilised remains of any particular group of animals which lived during

a limited period of the earth's history, and in a limited area, depends

upon at least a fivefold combination of chances. Now, if we take each of

these chances separately as only ten to one against us (and some are

certainly more than this), then the actual chance against our finding

the fossil remains, say of any one order of mammalia, or of land plants,

at any particular geological horizon, will be about a hundred thousand

to one.

It may be said, if the chances are so great, how is it that we find such

immense numbers of fossil species exceeding in number, in some groups,

all those that are now living? But this is exactly what we should

expect, because the number of species of organisms that have ever lived

upon the earth, since the earliest geological times, will probably be

many hundred times greater than those now existing of which we have any

knowledge; and hence the enormous gaps and chasms in the geological

record of extinct forms is not to be wondered at. Yet, notwithstanding

these chasms in our knowledge, if evolution is true, there ought to have

been, on the whole, progression in all the chief types of life. The

higher and more specialised forms should have come into existence later

than the lower and more generalised forms; and however fragmentary the

portions we possess of the whole tree of life upon the earth, they ought

to show us broadly that such a progressive evolution has taken place. We

have seen that in some special groups, already referred to, such a

progression is clearly visible, and we will now cast a hasty glance over

the entire series of fossil forms, in order to see if a similar

progression is manifested by them as a whole.

\_The Progressive Development of Plants.\_

Ever since fossil plants have been collected and studied, the broad fact

has been apparent that the early plants--those of the Coal

formation--were mainly cryptogamous, while in the Tertiary deposits the

higher flowering plants prevailed. In the intermediate secondary epoch

the gymnosperms--cycads and coniferae--formed a prominent part of the

vegetation, and as these have usually been held to be a kind of

transition form between the flowerless and flowering plants, the

geological succession has always, broadly speaking, been in accordance

with the theory of evolution. Beyond this, however, the facts were very

puzzling. The highest cryptogams--ferns, lycopods, and

equisetaceae--appeared suddenly, and in immense profusion in the Coal

formation, at which period they attained a development they have never

since surpassed or even equalled; while the highest plants--the

dicotyledonous and monocotyledonous angiosperms--which now form the bulk

of the vegetation of the world, and exhibit the most wonderful

modifications of form and structure, were almost unknown till the

Tertiary period, when they suddenly appeared in full development, and,

for the most part, under the same generic forms as now exist.

During the latter half of the present century, however, great additions

have been made to our knowledge of fossil plants; and although there

are still indications of vast gaps in our knowledge, due, no doubt, to

the very exceptional conditions required for the preservation of plant

remains, we now possess evidence of a more continuous development of the

various types of vegetation. According to Mr. Lester F. Ward, between

8000 and 9000 species of fossil plants have been described or indicated;

and, owing to the careful study of the nervation of leaves, a large

number of these are referable to their proper orders or genera, and

therefore give us some notion--which, though very imperfect, is probably

accurate in its main outlines--of the progressive development of

vegetation on the earth.[191] The following is a summary of the facts as

given by Mr. Ward:--

The lowest forms of vegetable life--the cellular plants--have been found

in Lower Silurian deposits in the form of three species of marine algae;

and in the whole Silurian formation fifty species have been recognised.

We cannot for a moment suppose, however, that this indicates the first

appearance of vegetable life upon the earth, for in these same Lower

Silurian beds the more highly organised vascular cryptogams appear in

the form of rhizocarps--plants allied to Marsilea and Azolla,--and a

very little higher, ferns, lycopods, and even conifers appear. We have

indications, however, of a still more ancient vegetation, in the

carbonaceous shales and thick beds of graphite far down in the Middle

Laurentian, since there is no other known agency than the vegetable cell

by means of which carbon can be extracted from the atmosphere and fixed

in the solid state. These great beds of graphite, therefore, imply the

existence of abundance of vegetable life at the very commencement of the

era of which we have any geological record.[192]

Ferns, as already stated, begin in the Middle Silurian formation with

the Eopteris Morrieri. In the Devonian, we have 79 species, in the

Carboniferous 627, and in the Permian 186 species; after which fossil

ferns diminish greatly, though they are found in every formation; and

the fact that fully 3000 living species are known, while the richest

portion of the Tertiary in fossil plants--the Miocene--- has only

produced 87 species, will serve to indicate the extreme imperfection of

the geological record.

The Equisetaceae (horsetails) which also first appear in the Silurian and

reach their maximum development in the Coal formation, are, in all

succeeding formations, far less numerous than ferns, and only thirty

living species are known. Lycopodiaceae, though still more abundant in

the Coal formation, are very rarely found in any succeeding deposit,

though the living species are tolerably numerous, about 500 having been

described. As we cannot suppose them to have really diminished and then

increased again in this extraordinary manner, we have another indication

of the exceptional nature of plant preservation and the extreme and

erratic character of the imperfection of the record.

Passing now to the next higher division of plants--the gymnosperms--we

find Coniferae appearing in the Upper Silurian, becoming tolerably

abundant in the Devonian, and reaching a maximum in the Carboniferous,

from which formation more than 300 species are known, equal to the

number recorded as now living. They occur in all succeeding formations,

being abundant in the Oolite, and excessively so in the Miocene, from

which 250 species have been described. The allied family of gymnosperms,

the Cycadaceae, first appear in the Carboniferous era, but very

scantily; are most abundant in the Oolite, from which formation 116

species are known, and then steadily diminish to the Tertiary, although

there are seventy-five living species.

We now come to the true flowering plants, and we first meet with

monocotyledons in the Carboniferous and Permian formations. The

character of these fossils was long disputed, but is now believed to be

well established; and the sub-class continues to be present in small

numbers in all succeeding deposits, becoming rather plentiful in the

Upper Cretaceous, and very abundant in the Eocene and Miocene. In the

latter formation 272 species have been discovered; but the 116 species

in the Eocene form a larger proportion of the total vegetation of the

period.

True dicotyledons appear very much later, in the Cretaceous period, and

only in its upper division, if we except a single species from the

Urgonian beds of Greenland. The remarkable thing is that we here find

the sub-class fully developed and in great luxuriance of types, all the

three divisions--Apetalae, Polypetalae, and Gamopetalae--being

represented, with a total of no less than 770 species. Among them are

such familiar forms as the poplar, the birch, the beech, the sycamore,

and the oak; as well as the fig, the true laurel, the sassafras, the

persimmon, the maple, the walnut, the magnolia, and even the apple and

the plum tribes. Passing on to the Tertiary period the numbers increase,

till they reach their maximum in the Miocene, where more than 2000

species of dicotyledons have been discovered. Among these the

proportionate number of the higher gamopetalae has slightly increased,

but is considerably less than at the present day.

\_Possible Cause of sudden late Appearance of Exogens.\_

The sudden appearance of fully developed exogenous flowering plants in

the Cretaceous period is very analogous to the equally sudden appearance

of all the chief types of placental mammalia in the Eocene; and in both

cases we must feel sure that this suddenness is only apparent, due to

unknown conditions which have prevented their preservation (or their

discovery) in earlier formations. The case of the dicotyledonous plants

is in some respects the most extraordinary, because in the earlier

Mesozoic formations we appear to have a fair representation of the flora

of the period, including such varied forms as ferns, equisetums, cycads,

conifers, and monocotyledons. The only hint at an explanation of this

anomaly has been given by Mr. Ball, who supposes that all these groups

inhabited the lowlands, where there was not only excessive heat and

moisture, but also a superabundance of carbonic acid in the

atmosphere--conditions under which these groups had been developed, but

which were prejudicial to the dicotyledons. These latter are supposed to

have originated on the high table-lands and mountain ranges, in a rarer

and drier atmosphere in which the quantity of carbonic acid gas was much

less; and any deposits formed in lake beds at high altitudes and at such

a remote epoch have been destroyed by denudation, and hence we have no

record of their existence.[193]

During a few weeks spent recently in the Rocky Mountains, I was struck

by the great scarcity of monocotyledons and ferns in comparison with

dicotyledons--a scarcity due apparently to the dryness and rarity of the

atmosphere favouring the higher groups. If we compare Coulter's \_Rocky

Mountain Botany\_ with Gray's \_Botany of the Northern (East) United

States\_, we have two areas which differ chiefly in the points of

altitude and atmospheric moisture. Unfortunately, in neither of these

works are the species consecutively numbered; but by taking the pages

occupied by the two divisions of dicotyledons on the one hand,

monocotyledons and ferns on the other, we can obtain a good

approximation. In this way we find that in the flora of the

North-Eastern States the monocotyledons and ferns are to the

dicotyledons in the proportion of 45 to 100; in the Rocky Mountains they

are in the proportion of only 34 to 100; while if we take an exclusively

Alpine flora, as given by Mr. Ball, there are not one-fifth as many

monocotyledons as dicotyledons. These facts show that even at the

present day elevated plateaux and mountains are more favourable to

dicotyledons than to monocotyledons, and we may, therefore, well suppose

that the former originated within such elevated areas, and were for long

ages confined to them. It is interesting to note that their richest

early remains have been found in the central regions of the North

American continent, where they now, proportionally, most abound, and

where the conditions of altitude and a dry atmosphere were probably

present at a very early period.

[Illustration: FIG. 34.--Diagram illustrating the Geological

Distribution of Plants.]

The diagram (Fig. 34), slightly modified from one given by Mr. Ward,

will illustrate our present knowledge of the development of the

vegetable kingdom in geological time. The shaded vertical bands exhibit

the proportions of the fossil forms actually discovered, while the

outline extensions are intended to show what we may fairly presume to

have been the approximate periods of origin, and progressive increase of

the number of species, of the chief divisions of the vegetable kingdom.

These seem to accord fairly well with their respective grades of

development, and thus offer no obstacle to the acceptance of the belief

in their progressive evolution.

\_Geological Distribution of Insects.\_

The marvellous development of insects into such an endless variety of

forms, their extreme specialisation, and their adaptation to almost

every possible condition of life, would almost necessarily imply an

extreme antiquity. Owing, however, to their small size, their lightness,

and their usually aerial habits, no class of animals has been so

scantily preserved in the rocks; and it is only recently that the whole

of the scattered material relating to fossil insects and their allies

have been brought together by Mr. Samuel H. Scudder of Boston, and we

have thus learned their bearing on the theory of evolution.[194]

The most striking fact which presents itself on a glance at the

distribution of fossil insects, is the completeness of the

representation of all the chief types far back in the Secondary period,

at which time many of the existing families appear to have been

perfectly differentiated. Thus in the Lias we find dragonflies

"apparently as highly specialised as to-day, no less than four tribes

being present." Of beetles we have undoubted Curculionidae from the Lias

and Trias; Chrysomelidae in the same deposits; Cerambycidae in the

Oolites; Scarabaeidae in the Lias; Buprestidae in the Trias; Elateridae,

Trogositidae, and Nitidulidae in the Lias; Staphylinidae in the English

Purbecks; while Hydrophilidae, Gyrinidae, and Carabidae occur in the

Lias. All these forms are well represented, but there are many other

families doubtfully identified in equally ancient rocks. Diptera of the

families Empidae, Asilidae, and Tipulidae have been found as far back as

the Lias. Of Lepidoptera, Sphingidae and Tineidae have been found in

the Oolite; while ants, representing the highly specialised Hymenoptera,

have occurred in the Purbeck and Lias.

This remarkable identity of the families of very ancient with those of

existing insects is quite comparable with the apparently sudden

appearance of existing genera of trees in the Cretaceous epoch. In both

cases we feel certain that we must go very much farther back in order to

find the ancestral forms from which they were developed, and that at any

moment some fresh discovery may revolutionise our ideas as to the

antiquity of certain groups. Such a discovery was made while Mr.

Scudder's work was passing through the press. Up to that date all the

existing orders of true insects appeared to have originated in the

Trias, the alleged moth and beetle of the Coal formation having been

incorrectly determined. But now, undoubted remains of beetles have been

found in the Coal measures of Silesia, thus supporting the

interpretation of the borings in carboniferous trees as having been made

by insects of this order, and carrying back this highly specialised form

of insect life well into Palaeozoic times. Such a discovery renders all

speculation as to the origin of true insects premature, because we may

feel sure that all the other orders of insects, except perhaps

hymenoptera and lepidoptera, were contemporaneous with the highly

specialised beetles.

The less highly organised terrestrial arthropoda--the Arachnida and

Myriapoda--are, as might be expected, much more ancient. A fossil spider

has been found in the Carboniferous, and scorpions in the Upper Silurian

rocks of Scotland, Sweden, and the United States. Myriapoda have been

found abundantly in the Carboniferous and Devonian formations; but all

are of extinct orders, exhibiting a more generalised structure than

living forms.

Much more extraordinary, however, is the presence in the Palaeozoic

formations of ancestral forms of true insects, termed by Mr. Scudder

Palaeodictyoptera. They consist of generalised cockroaches and

walking-stick insects (Orthopteroidea); ancient mayflies and allied

forms, of which there are six families and more than thirty genera

(Neuropteroidea); three genera of Hemipteroidea resembling various

Homoptera and Hemiptera, mostly from the Carboniferous formation, a few

from the Devonian, and one ancestral cockroach (Palaeoblattina) from

the Middle Silurian sandstone of France. If this occurrence of a true

hexapod insect from the Middle Silurian be really established, taken in

connection with the well-defined Coleoptera from the Carboniferous, the

origin of the entire group of terrestrial arthropoda is necessarily

thrown back into the Cambrian epoch, if not earlier. And this cannot be

considered improbable in view of the highly differentiated land

plants--ferns, equisetums, and lycopods--in the Middle or Lower

Silurian, and even a conifer (Cordaites Robbii) in the Upper Silurian;

while the beds of graphite in the Laurentian were probably formed from

terrestrial vegetation.

On the whole, then, we may affirm that, although the geological record

of the insect life of the earth is exceptionally imperfect, it yet

decidedly supports the evolution hypothesis. The most specialised order,

Lepidoptera, is the most recent, only dating back to the Oolite; the

Hymenoptera, Diptera, and Homoptera go as far as the Lias; while the

Orthoptera and Neuroptera extend to the Trias. The recent discovery of

Coleoptera in the Carboniferous shows, however, that the preceding

limits are not absolute, and will probably soon be overpassed. Only the

more generalised ancestral forms of winged insects have been traced back

to Silurian time, and along with them the less highly organised

scorpions; facts which serve to show us the extreme imperfection of our

knowledge, and indicate possibilities of a world of terrestrial life in

the remotest Palaeozoic times.

\_Geological Succession of Vertebrata.\_

The lowest forms of vertebrates are the fishes, and these appear first

in the geological record in the Upper Silurian formation. The most

ancient known fish is a Pteraspis, one of the bucklered ganoids or

plated fishes--by no means a very low type--allied to the sturgeon

(Accipenser) and alligator-gar (Lepidosteus), but, as a group, now

nearly extinct. Almost equally ancient are the sharks, which under

various forms still abound in our seas. We cannot suppose these to be

nearly the earliest fishes, especially as the two lowest orders, now

represented by the Amphioxus or lancelet and the lampreys, have not yet

been found fossil. The ganoids were greatly developed in the Devonian

era, and continued till the Cretaceous, when they gave way to the true

osseous fishes, which had first appeared in the Jurassic period, and

have continued to increase till the present day. This much later

appearance of the higher osseous fishes is quite in accordance with

evolution, although some of the very lowest forms, the lancelet and the

lampreys, together with the archaic ceratodus, have survived to our

time.

The Amphibia, represented by the extinct labyrinthodons, appear first in

the Carboniferous rocks, and these peculiar forms became extinct early

in the Secondary period. The labyrinthodons were, however, highly

specialised, and do not at all indicate the origin of the class, which

may be as ancient as the lower forms of fishes. Hardly any recognisable

remains of our existing groups--the frogs, toads, and salamanders--are

found before the Tertiary period, a fact which indicates the extreme

imperfection of the record as regards this class of animals.

True reptiles have not been found till we reach the Permian where

Prohatteria and Proterosaurus occur, the former closely allied to the

lizard-like Sphenodon of New Zealand, the latter having its nearest

allies in the same group of reptiles--Rhyncocephala, other forms of

which occur in the Trias. In this last-named formation the earliest

crocodiles--Phytosaurus (Belodon) and Stagonolepis occur, as well as the

earliest tortoises--Chelytherium, Proganochelys, and Psephoderma.[195]

Fossil serpents have been first found in the Cretaceous formation, but

the conditions for the preservation of these forms have evidently been

unfavourable, and the record is correspondingly incomplete. The marine

Plesiosauri and Ichthyosauri, the flying Pterodactyles, the terrestrial

Iguanodon of Europe, and the huge Atlantosaurus of Colorado--the largest

land animal that has ever lived upon the earth[196]--all belong to

special developments of the reptilian type which flourished during the

Secondary epoch, and then became extinct.

Birds are among the rarest of fossils, due, no doubt, to their aerial

habits removing them from the ordinary dangers of flood, bog, or ice

which overwhelm mammals and reptiles, and also to their small specific

gravity which keeps them floating on the surface of water till devoured.

Their remains were long confined to Tertiary deposits, where many living

genera and a few extinct forms have been found. The only birds yet known

from the older rocks are the toothed birds (Odontornithes) of the

Cretaceous beds of the United States, belonging to two distinct families

and many genera; a penguin-like form (Enaliornis) from the Upper

Greensand of Cambridge; and the well-known long-tailed Archaeopteryx

from the Upper Oolite of Bavaria. The record is thus imperfect and

fragmentary in the extreme; but it yet shows us, in the few birds

discovered in the older rocks, more primitive and generalised types,

while the Tertiary birds had already become specialised like those

living, and had lost both the teeth and the long vertebral tail, which

indicate reptilian affinities in the earlier Mammalia have been found,

as already stated, as far back as the Trias formation, in Europe in the

United States and in South Africa, all being very small, and belonging

either to the Marsupial order, or to some still lower and more

generalised type, out of which both Marsupials and Insectivora were

developed. Other allied forms have been found in the Lower and Upper

Oolite both of Europe and the United States. But there is then a great

gap in the whole Cretaceous formation, from which no mammal has been

obtained, although both in the Wealden and the Upper Chalk in Europe,

and in the Upper Cretaceous deposits of the United States an abundant

and well-preserved terrestrial flora has been discovered. Why no mammals

have left their remains here it is impossible to say. We can only

suppose that the limited areas in which land plants have been so

abundantly preserved, did not present the conditions which are needed

for the fossilisation and preservation of mammalian remains.

When we come to the Tertiary formation, we find mammals in abundance;

but a wonderful change has taken place. The obscure early types have

disappeared, and we discover in their place a whole series of forms

belonging to existing orders, and even sometimes to existing families.

Thus, in the Eocene we have remains of the opossum family; bats

apparently belonging to living genera; rodents allied to the South

American cavies and to dormice and squirrels; hoofed animals belonging

to the odd-toed and even-toed groups; and ancestral forms of cats,

civets, dogs, with a number of more generalised forms of carnivora.

Besides these there are whales, lemurs, and many strange ancestral forms

of proboscidea.[197]

The great diversity of forms and structures at so remote an epoch would

require for their development an amount of time, which, judging by the

changes that have occurred in other groups, would carry us back far into

the Mesozoic period. In order to understand why we have no record of

these changes in any part of the world, we must fall back upon some such

supposition as we made in the case of the dicotyledonous plants.

Perhaps, indeed, the two cases are really connected, and the upland

regions of the primeval world, which saw the development of our higher

vegetation, may have also afforded the theatre for the gradual

development of the varied mammalian types which surprise us by their

sudden appearance in Tertiary times.

[Illustration: GEOLOGICAL DISTRIBUTION OF MAMMALIA.]

Notwithstanding these irregularities and gaps in the record, the

accompanying table, summarising our actual knowledge of the geological

distribution of the five classes of vertebrata, exhibits a steady

progression from lower to higher types, excepting only the deficiency in

the bird record which is easily explained. The comparative perfection of

type in which each of these classes first appears, renders it certain

that the origin of each and all of them must be sought much farther back

than any records which have yet been discovered. The researches of

palaeontologists and embryologists indicate a reptilian origin for birds

and mammals, while reptiles and amphibia arose, perhaps independently,

from fishes.

\_Concluding Remarks.\_

The brief review we have now taken of the more suggestive facts

presented by the geological succession of organic forms, is sufficient

to show that most, if not all, of the supposed difficulties which it

presents in the way of evolution, are due either to imperfections in the

geological record itself, or to our still very incomplete knowledge of

what is really recorded in the earth's crust. We learn, however, that

just as discovery progresses, gaps are filled up and difficulties

disappear; while, in the case of many individual groups, we have already

obtained all the evidence of progressive development that can reasonably

be expected. We conclude, therefore, that the geological difficulty has

now disappeared; and that this noble science, when properly understood,

affords clear and weighty evidence of evolution.

FOOTNOTES:

[Footnote 183: The reader who desires to understand this subject more

fully, should study chap. x. of the \_Origin of Species\_, and chap. xiv.

of Sir Charles Lyell's \_Principles of Geology\_.]

[Footnote 184: On "Stagonolepis Robertsoni and on the Evolution of the

Crocodilia," in \_Q.J. of Geological Society\_, 1875; and abstract in

\_Nature\_, vol. xii. p. 38.]

[Footnote 185: From a paper by Messrs. Scott and Osborne, "On the Origin

and Development of the Rhinoceros Group," read before the British

Association in 1883.]

[Footnote 186: American Addresses, pp. 73-76.]

[Footnote 187: Lecture on the Introduction and Succession of Vertebrate

Life in America, \_Nature\_, vol. xvi. p. 471.]

[Footnote 188: \_Nature\_, vol. xxv. p. 84.]

[Footnote 189: See \_The Mammalia in their Relation to Primeval Times\_,

p. 102.]

[Footnote 190: For a brief enumeration and description of these fossils,

see the author's \_Geographical Distribution of Animals\_, vol. i. p.

146.]

[Footnote 191: Sketch of Palaeobotany in Fifth Annual Report of U.S.

Geological Survey, 1883-84, pp. 363-452, with diagrams. Sir J. William

Dawson, speaking of the value of leaves for the determination of fossil

plants, says: "In my own experience I have often found determinations of

the leaves of trees confirmed by the discovery of their fruits or of the

structure of their stems. Thus, in the rich cretaceous plant-beds of the

Dunvegan series, we have beech-nuts associated in the same bed with

leaves referred to \_Fagus\_. In the Laramie beds I determined many years

ago nuts of the \_Trapa\_ or water-chestnut, and subsequently Lesquereux

found in beds in the United States leaves which he referred to the same

genus. Later, I found in collections made on the Red Deer River of

Canada my fruits and Lesquereux's leaves on the same slab. The presence

of trees of the genera \_Carya\_ and \_Juglans\_ in the same formation was

inferred from their leaves, and specimens have since been obtained of

silicified wood with the microscopic structure of the modern butternut.

Still we are willing to admit that determinations from leaves alone are

liable to doubt."--\_The Geological History of Plants\_, p. 196.]

[Footnote 192: Sir J. William Dawson's \_Geological History of Plants\_,

p. 18.]

[Footnote 193: "On the Origin of the Flora of the European Alps," \_Proc.

of Roy. Geog. Society\_, vol. i. (1879), pp. 564-588.]

[Footnote 194: Systematic Review of our Present Knowledge of Fossil

Insects, including Myriapods and Arachnids (\_Bull. of U.S. Geol.

Survey\_, No. 31, Washington, 1886).]

[Footnote 195: For the facts as to the early appearance of the above

named groups of reptiles I am indebted to Mr. E. Lydekker of the

Geological Department of the Natural History Museum.]

[Footnote 196: According to Professor Marsh this creature was 50 or 60

feet long, and when erect, at least 30 feet in height. It fed upon the

foliage of the mountain forests of the Cretaceous epoch, the remains of

which are preserved with it.]

[Footnote 197: For fuller details, see the author's \_Geographical

Distribution of Animals\_, and Heilprin's \_Geographical and Geological

Distribution of Animals\_.]

CHAPTER XIV

FUNDAMENTAL PROBLEMS IN RELATION TO VARIATION AND HEREDITY

Fundamental difficulties and objections--Mr. Herbert Spencer's

factors of organic evolution--Disuse and effects of withdrawal

of natural selection--Supposed effects of disuse among wild

animals--Difficulty as to co-adaptation of parts by variation

and selection--Direct action of the environment--The American

school of evolutionists--Origin of the feet of the

ungulates--Supposed action of animal intelligence--Semper on the

direct influence of the environment--Professor Geddes's theory

of variation in plants--Objections to the theory--On the origin

of spines--Variation and selection overpower the effects of use

and disuse--Supposed action of the environment in imitating

variations--Weismann's theory of heredity--The cause of

variation--The non-heredity of acquired characters--The theory

of instinct--Concluding remarks.

Having now set forth and illustrated at some length the most important

of the applications of the development hypothesis in the explanation of

the broader and more generally interesting phenomena presented by the

organic world, we propose to discuss some of the more fundamental

problems and difficulties which have recently been adduced by eminent

naturalists. It is the more necessary to do this, because there is now a

tendency to minimise the action of natural selection in the production

of organic forms, and to set up in its place certain fundamental

principles of variation or laws of growth, which it is urged are the

real originators of the several lines of development, and of most of the

variety of form and structure in the vegetable and animal kingdoms.

These views have, moreover, been seized upon by popular writers to throw

doubt and discredit on the whole theory of evolution, and especially on

Darwin's presentation of that theory, to the bewilderment of the general

public, who are quite unable to decide how far the new views, even if

well established, tend to subvert the Darwinian theory, or whether they

are really more than subsidiary parts of it, and quite powerless without

it to produce any effect whatever.

The writers whose special views we now propose to consider are: (1) Mr.

Herbert Spencer, on modification of structures arising from modification

of functions, as set forth in his \_Factors of Organic Evolution\_. (2)

Dr. E.D. Cope, who advocates similar views in detail, in his work

entitled \_The Origin of the Fittest\_, and may be considered the head of

a school of American naturalists who minimise the agency of natural

selection. (3) Dr. Karl Semper, who has especially studied the direct

influence of the environment in the whole animal kingdom, and has set

forth his views in a volume on \_The Natural Conditions of Existence as

they Affect Animal Life\_. (4) Mr. Patrick Geddes, who urges that

fundamental laws of growth, and the antagonism of vegetative and

reproductive forces, account for much that has been imputed to natural

selection.

We will now endeavour to ascertain what are the more important facts and

arguments adduced by each of the above writers, and how far they offer a

substitute for the action of natural selection; having done which, a

brief account will be given of the views of Dr. Aug. Weismann, whose

theory of heredity will, if established, strike at the very root of the

arguments of the first three of the writers above referred to.

\_Mr. Herbert Spencer's Factors of Organic Evolution.\_

Mr. Spencer, while fully recognising the importance and wide range of

the principle of natural selection, thinks that sufficient weight has

not been given to the effects of use and disuse as a factor in

evolution, or to the direct action of the environment in determining or

modifying organic structures. As examples of the former class of

actions, he adduces the decreased size of the jaws in the civilised

races of mankind, the inheritance of nervous disease produced by

overwork, the great and inherited development of the udders in cows and

goats, and the shortened legs, jaws, and snout in improved races of

pigs--the two latter examples being quoted from Mr. Darwin,--and other

cases of like nature. As examples of the latter, Mr. Darwin is again

quoted as admitting that there are many cases in which the action of

similar conditions appears to have produced corresponding changes in

different species; and we have a very elaborate discussion of the direct

action of the medium in modifying the protoplasm of simple organisms, so

as to bring about the difference between the outer surface and the inner

part that characterises the cells or other units of which they are

formed.

Now, although this essay did little more than bring together facts which

had been already adduced by Mr. Darwin or by Mr. Spencer himself, and

lay stress upon their importance, its publication in a popular review

was immediately seized upon as "an avowed and definite declaration

against some of the leading ideas on which the Mechanical Philosophy

depends," and as being "fatal to the adequacy of the Mechanical

Philosophy as any explanation of organic evolution,"[198]--an expression

of opinion which would be repudiated by every Darwinian. For, even

admitting the interpretation which Mr. Spencer puts on the facts he

adduces, they are all included in the causes which Darwin himself

recognised as having acted in bringing about the infinitude of forms in

the organic world. In the concluding chapter of the \_Origin of Species\_

he says: "I have now recapitulated the facts and considerations which

have thoroughly convinced me that species have been modified during a

long course of descent. This has been effected chiefly through the

natural selection of numerous successive, slight, favourable variations;

aided in an important manner by the inherited effects of the use and

disuse of parts; and in an unimportant manner--that is, in relation to

adaptive structures whether past or present, by the direct action of

external conditions, and by variations which seem to us, in our

ignorance, to arise spontaneously." This passage, summarising Darwin's

whole inquiry, and explaining his final point of view, shows how very

inaccurate may be the popular notion, as expressed by the Duke of

Argyll, of any supposed additions to the causes of change of species as

recognised by Darwin.

But, as we shall see presently, there is now much reason to believe

that the supposed inheritance of acquired modifications--that is, of the

effects of use and disuse, or of the direct influence of the

environment--is not a fact; and if so, the very foundation is taken away

from the whole class of objections on which so much stress is now laid.

It therefore becomes important to inquire whether the facts adduced by

Darwin, Spencer, and others, do really necessitate such inheritance, or

whether any other interpretation of them is possible. I believe there is

such an interpretation; and we will first consider the cases of disuse

on which Mr. Spencer lays most stress.

The cases Mr. Spencer adduces as demonstrating the effects of disuse in

diminishing the size and strength of organs are, the diminished size of

the jaws in the races of civilised men, and the diminution of the

muscles used in closing the jaws in the case of pet-dogs fed for

generations on soft food. He argues that the minute reduction in any one

generation could not possibly have been useful, and, therefore, not the

subject of natural selection; and against the theory of correlation of

the diminished jaw with increased brain in man, he urges that there are

cases of large brain development, accompanied by jaws above the average

size. Against the theory of economy of nutrition in the case of the

pet-dogs, he places the abundant food of these animals which would

render such economy needless.

But neither he nor Mr. Darwin has considered the effects of the

withdrawal of the action of natural selection in keeping up the parts in

question to their full dimensions, which, of itself, seems to me quite

adequate to produce the results observed. Recurring to the evidence,

adduced in Chapter III, of the constant variation occurring in all parts

of the organism, while selection is constantly acting on these

variations in eliminating all that fall below the best working standard,

and preserving only those that are fully up to it; and, remembering

further, that, of the whole number of the increase produced annually,

only a small percentage of the best adapted can be preserved, we shall

see that every useful organ will be kept up nearly to its higher limit

of size and efficiency. Now Mr. Galton has proved experimentally that,

when any part has thus been increased (or diminished) by selection,

there is in the offspring a strong tendency to revert to a mean or

average size, which tends to check further increase. And this mean

appears to be, not the mean of the actual existing individuals but a

lower mean, or that from which they had been recently raised by

selection.[199] He calls this the law of "Regression towards

Mediocrity," and it has been proved by experiments with vegetables and

by observations on mankind. This regression, in every generation, takes

place even when both parents have been selected for their high

development of the organ in question; but when there is no such

selection, and crosses are allowed among individuals of every grade of

development, the deterioration will be very rapid; and after a time not

only will the average size of the part be greatly reduced, but the

instances of full development will become very rare. Thus what Weismann

terms "panmixia," or free intercrossing, will co-operate with Galton's

law of "regression towards mediocrity," and the result will be that,

whenever selection ceases to act on any part or organ which has

heretofore been kept up to a maximum of size and efficiency, the organ

in question will rapidly decrease till it reaches a mean value

considerably below the mean of the progeny that has usually been

produced each year, and very greatly below the mean of that portion

which has survived annually; and this will take place by the general law

of heredity, and quite irrespective of any \_use\_ or \_disuse\_ of the part

in question. Now, no observations have been adduced by Mr. Spencer or

others, showing that the average amount of change supposed to be due to

\_disuse\_ is greater than that due to the law of regression towards

mediocrity; while even if it were somewhat greater, we can see many

possible contributory causes to its production. In the case of civilised

man's diminished jaw, there may well be some correlation between the jaw

and the brain, seeing that increased mental activity would lead to the

withdrawal of blood and of nervous energy from adjacent parts, and might

thus lead to diminished growth of those parts in the individual. And in

the case of pet-dogs, the selection of small or short-headed individuals

would imply the unconscious selection of those with less massive

temporal muscles, and thus lead to the concomitant reduction of those

muscles. The amount of reduction observed by Darwin in the wing-bones of

domestic ducks and poultry, and in the hind legs of tame rabbits, is

very small, and is certainly no greater than the above causes will well

account for; while so many of the external characters of all our

domestic animals have been subject to long-continued artificial

selection, and we are so ignorant of the possible correlations of

different parts, that the phenomena presented by them seem sufficiently

explained without recurrence to the assumption that any changes in the

individual, due to disuse, are inherited by the offspring.

\_Supposed Effects of Disuse among Wild Animals.\_

It may be urged, however, that among wild animals we have many undoubted

results of disuse much more pronounced than those among domestic kinds,

results which cannot be explained by the causes already adduced. Such

are the reduced size of the wings of many birds on oceanic islands; the

abortion of the eyes in many cave animals, and in some which live

underground; and the loss of the hind limbs in whales and in some

lizards. These cases differ greatly in the amount of the reduction of

parts which has taken place, and may be due to different causes. It is

remarkable that in some of the birds of oceanic islands the reduction is

little if at all greater than in domestic birds, as in the water-hen of

Tristan d'Acunha. Now if the reduction of wing were due to the

hereditary effects of disuse, we should expect a very much greater

effect in a bird inhabiting an oceanic island than in a domestic bird,

where the disuse has been in action for an indefinitely shorter period.

In the case of many other birds, however--as some of the New Zealand

rails and the extinct dodo of Mauritius--the wings have been reduced to

a much more rudimentary condition, though it is still obvious that they

were once organs of flight; and in these cases we certainly require some

other causes than those which have reduced the wings of our domestic

fowls. One such cause may have been of the same nature as that which has

been so efficient in reducing the wings of the insects of oceanic

islands--the destruction of those which, during the occasional use of

their wings, were carried out to sea. This form of natural selection may

well have acted in the case of birds whose powers of flight were

already somewhat reduced, and to whom, there being no enemies to escape

from, their use was only a source of danger. We may thus, perhaps,

account for the fact that many of these birds retain small but useless

wings with which they never fly; for, the wings having been reduced to

this functionless condition, no power could reduce them further except

correlation of growth or economy of nutrition, causes which only rarely

come into play.

The complete loss of eyes in some cave animals may, perhaps, be

explained in a somewhat similar way. Whenever, owing to the total

darkness, they became useless, they might also become injurious, on

account of their delicacy of organisation and liability to accidents and

disease; in which case natural selection would begin to act to reduce,

and finally abort them; and this explains why, in some cases, the

rudimentary eye remains, although completely covered by a protective

outer skin. Whales, like moas and cassowaries, carry us back to a remote

past, of whose conditions we know too little for safe speculation. We

are quite ignorant of the ancestral forms of either of these groups, and

are therefore without the materials needful for determining the steps by

which the change took place, or the causes which brought it about.[200]

On a review of the various examples that have been given by Mr. Darwin

and others of organs that have been reduced or aborted, there seems too

much diversity in the results for all to be due to so direct and uniform

a cause as the individual effects of disuse accumulated by heredity. For

if that were the only or chief efficient cause, and a cause capable of

producing a decided effect during the comparatively short period of the

existence of animals in a state of domestication, we should expect to

find that, in wild species, all unused parts or organs had been reduced

to the smallest rudiments, or had wholly disappeared. Instead of this we

find various grades of reduction, indicating the probable result of

several distinct causes, sometimes acting separately, sometimes in

combination, such as those we have already pointed out.

And if we find no positive evidence of \_disuse\_, acting by its direct

effect on the individual, being transmitted to the offspring, still less

can we find such evidence in the case of the \_use\_ of organs. For here

the very fact of \_use\_, in a wild state, implies \_utility\_, and utility

is the constant subject for the action of natural selection; while among

domestic animals those parts which are exceptionally used are so used in

the service of man, and have thus become the subjects of artificial

selection. Thus "the great and inherited development of the udders in

cows and goats," quoted by Spencer from Darwin, really affords no proof

of inheritance of the increase due to use, because, from the earliest

period of the domestication of these animals, abundant milk-production

has been highly esteemed, and has thus been the subject of selection;

while there are no cases among wild animals that may not be better

explained by variation and natural selection.

\_Difficulty as to Co-adaptation of Parts by Variation and Selection.\_

Mr. Spencer again brings forward this difficulty, as he did in his

\_Principles of Biology\_ twenty-five years ago, and urges that all the

adjustments of bones, muscles, blood-vessels, and nerves which would be

required during, for example, the development of the neck and fore-limbs

of the giraffe, could not have been effected by "simultaneous fortunate

spontaneous variations." But this difficulty is fully disposed of by the

facts of simultaneous variation adduced in our third chapter, and has

also been specially considered in Chapter VI, p. 127. The best answer to

this objection may, perhaps, be found in the fact that the very thing

said to be impossible by variation and natural selection has been again

and again effected by variation and artificial selection. During the

process of formation of such breeds as the greyhound or the bulldog, of

the race-horse and carthorse, of the fantail pigeon or the otter-sheep,

many co-ordinate adjustments have been produced; and no difficulty has

occurred, whether the change has been effected by a single variation--as

in the last case named--or by slow steps, as in all the others. It seems

to be forgotten that most animals have such a surplus of vitality and

strength for all the ordinary occasions of life that any slight

superiority in one part can be at once utilised; while the moment any

want of balance occurs, variations in the insufficiently developed parts

will be selected to bring back the harmony of the whole organisation.

The fact that, in all domestic animals, variations do occur, rendering

them swifter or stronger, larger or smaller, stouter or slenderer, and

that such variations can be separately selected and accumulated for

man's purposes, is sufficient to render it certain that similar or even

greater changes may be effected by natural selection, which, as Darwin

well remarks, "acts on every internal organ, on every shade of

constitututional difference, on the whole machinery of life." The

difficulty as to co-adaptation of parts by variation and natural

selection appears to me, therefore, to be a wholly imaginary difficulty

which has no place whatever in the operations of nature.

\_Direct Action of the Environment.\_

Mr. Spencer's last objection to the wide scope given by Darwinians to

the agency of natural selection is, that organisms are acted upon by the

environment, which produces in them definite changes, and that these

changes in the individual are transmitted by inheritance, and thus

become increased in successive generations. That such changes are

produced in the individual there is ample evidence, but that they are

inherited independently of any form of selection or of reversion is

exceedingly doubtful, and Darwin nowhere expresses himself as satisfied

with the evidence. The two very strongest cases he mentions are the

twenty-nine species of American trees which all differed in a

corresponding way from their nearest European allies; and the American

maize which became changed after three generations in Europe. But in the

case of the trees the differences alleged may be partly due to

correlation with constitutional peculiarities dependent on climate,

especially as regards the deeper tint of the fading leaves and the

smaller size of the buds and seeds in America than in Europe; while the

less deeply toothed or serrated leaves in the American species are, in

our present complete ignorance of the causes and uses of serration,

quite as likely to be due to some form of adaptation as to any direct

action of the climate. Again, we are not told how many of the allied

species do not vary in this particular manner, and this is certainly an

important factor in any conclusion we may form on the question.

In the case of the maize it appears that one of the more remarkable and

highly selected American varieties was cultivated in Germany, and in

three years nearly all resemblance to the original parent was lost; and

in the sixth year it closely resembled a common European variety, but

was of somewhat more vigorous growth. In this case no selection appears

to have been practised, and the effects may have been due to that

"reversion to mediocrity" which invariably occurs, and is more

especially marked in the case of varieties which have been rapidly

produced by artificial selection. It may be considered as a partial

reversion to the wild or unimproved stock; and the same thing would

probably have occurred, though perhaps less rapidly, in America itself.

As this is stated by Darwin to be the most remarkable case known to him

"of the direct and prompt action of climate on a plant," we must

conclude that such direct effects have not been proved to be accumulated

by inheritance, independently of reversion or selection.

The remaining part of Mr. Spencer's essay is devoted to a consideration

of the hypothetical action of the environment on the lower organisms

which consist of simple cells or formless masses of protoplasm; and he

shows with great elaboration that the outer and inner parts of these

are necessarily subject to different conditions; and that the outer

actions of air or water lead to the formation of integuments, and

sometimes to other definite modifications of the surface, whence arise

permanent differences of structure. Although in these cases also it is

very difficult to determine how much is due to direct modification by

external agencies transmitted and accumulated by inheritance, and how

much to spontaneous variations accumulated by natural selection, the

probabilities in favour of the former mode of action are here greater,

because there is no differentiation of nutritive and reproductive cells

in these simple organisms; and it can be readily seen that any change

produced in the latter will almost certainly affect the next

generation.[201] We are thus carried back almost to the origin of life,

and can only vaguely speculate on what took place under conditions of

which we know so little.

\_The American School of Evolutionists.\_

The tentative views of Mr. Spencer which we have just discussed, are

carried much further, and attempts have been made to work them out in

great detail, by many American naturalists, whose best representative is

Dr. E.D. Cope of Philadelphia.[202] This school endeavours to explain

all the chief modifications of form in the animal kingdom by fundamental

laws of growth and the inherited effects of use and effort, returning,

in fact, to the teachings of Lamarck as being at least equally important

with those of Darwin.

The following extract will serve to show the high position claimed by

this school as original discoverers, and as having made important

additions to the theory of evolution:

"Wallace and Darwin have propounded as the cause of modification in

descent their law of natural selection. This law has been epitomised by

Spencer as the 'survival of the fittest.' This neat expression no doubt

covers the case, but it leaves the origin of the fittest entirely

untouched. Darwin assumes a 'tendency to variation' in nature, and it is

plainly necessary to do this, in order that materials for the exercise

of a selection should exist. Darwin and Wallace's law is then only

restrictive, directive, conservative, or destructive of something

already created. I propose, then, to seek for the originative laws by

which these subjects are furnished; in other words, for the causes of

the origin of the fittest."[203]

Mr. Cope lays great stress on the existence of a special developmental

force termed "bathmism" or growth-force, which acts by means of

retardation and acceleration "without any reference to fitness at all;"

that "instead of being controlled by fitness it is the controller of

fitness." He argues that "all the characteristics of generalised groups

from genera up (excepting, perhaps, families) have been evolved under

the law of acceleration and retardation," combined with some

intervention of natural selection; and that specific characters, or

species, have been evolved by natural selection with some assistance

from the higher law. He, therefore, makes species and genera two

absolutely distinct things, the latter not developed out of the former;

generic characters and specific characters are, in his opinion,

fundamentally different, and have had different origins, and whole

groups of species have been simultaneously modified, so as to belong to

another genus; whence he thinks it "highly probable that the same

specific form has existed through a succession of genera, and perhaps in

different epochs of geologic time."

Useful characters, he concludes, have been produced by the special

location of growth-force by use; useless ones have been produced by

location of growth-force without the influence of use. Another element

which determines the direction of growth-force, and which precedes use,

is effort; and "it is thought that effort becomes incorporated into the

metaphysical acquisitions of the parent, and is inherited with other

metaphysical qualities by the young, which, during the period of growth,

is much more susceptible to modifying influences, and is likely to

exhibit structural change in consequence."[204]

From these few examples of their teachings, it is clear that these

American evolutionists have departed very widely from the views of Mr.

Darwin, and in place of the well-established causes and admitted laws to

which he appeals have introduced theoretical conceptions which have not

yet been tested by experiments or facts, as well as metaphysical

conceptions which are incapable of proof. And when they come to

illustrate these views by an appeal to palaeontology or morphology, we

find that a far simpler and more complete explanation of the facts is

afforded by the established principles of variation and natural

selection. The confidence with which these new ideas are enunciated, and

the repeated assertion that without them Darwinism is powerless to

explain the origin of organic forms, renders it necessary to bestow a

little more time on the explanations they give us of well-known

phenomena with which, they assert, other theories are incompetent to

grapple.

As examples of use producing structural change, Mr. Cope adduces the

hooked and toothed beaks of the falcons and the butcher-birds, and he

argues that the fact of these birds belonging to widely different groups

proves that similarity of use has produced a similar structural result.

But no attempt is made to show any direct causal connection between the

use of a bill to cut or tear flesh and the development of a tooth on the

mandible. Such use might conceivably strengthen the bill or increase its

size, but not cause a special tooth-like outgrowth which was not present

in the ancestral thrush-like forms of the butcher-bird. On the other

hand, it is clear that any variations of the bill tending towards a hook

or tooth would give the possessor some advantage in seizing and tearing

its prey, and would thus be preserved and increased by natural

selection. Again, Mr. Cope urges the effects of a supposed "law of polar

or centrifugal growth" to counteract a tendency to unsymmetrical growth,

where one side of the body is used more than the other. But the

undoubted hurtfulness of want of symmetry in many important actions or

functions would rapidly eliminate any such tendency. When, however, it

has become useful, as in the case of the single enlarged claw of many

Crustacea, it has been preserved by natural selection.

\_Origin of the Feet of the Ungulates.\_

Perhaps the most original and suggestive of Mr. Cope's applications of

the theory of use and effort in modifying structure are, his chapters

"On the Origin of the Foot-Structure of the Ungulates;" and that "On the

Effect of Impacts and Strains on the Feet of Mammalia;" and they will

serve also to show the comparative merits of this theory and that of

natural selection in explaining a difficult case of modification,

especially as it is an explanation claimed as new and original when

first enunciated in 1881. Let us, then, see how he deals with the

problem.

The remarkable progressive change of a four or five-toed ancestor into

the one-toed horse, and the equally remarkable division of the whole

group of ungulate animals into the odd-toed and even-toed divisions, Mr.

Cope attempts to explain by the effects of impact and use among animals

which frequented hard or swampy ground respectively. On hard ground, it

is urged, the long middle toe would be most used and subjected to the

greatest strains, and would therefore acquire both strength and

development. It would then be still more exclusively used, and the extra

nourishment required by it would be drawn from the adjacent less-used

toes, which would accordingly diminish in size, till, after a long

series of changes, the records of which are so well preserved in the

American tertiary rocks, the true one-toed horse was developed. In soft

or swampy ground, on the other hand, the tendency would be to spread out

the foot so that there were two toes on each side. The two middle toes

would thus be most used and most subject to strains, and would,

therefore, increase at the expense of the lateral toes. There would be,

no doubt, an advantage in these two functional toes being of equal size,

so as to prevent twisting of the foot while walking; and variations

tending to bring this about would be advantageous, and would therefore

be preserved. Thus, by a parallel series of changes in another

direction, adapted to a distinct set of conditions, we should arrive at

the symmetrical divided hoofs of our deer and cattle. The fact that

sheep and goats are specially mountain and rock-loving animals may be

explained by their being a later modification, since the divided hoof

once formed is evidently well adapted to secure a firm footing on rugged

and precipitous ground, although it could hardly have been first

developed in such localities. Mr. Cope thus concludes: "Certain it is

that the length of the bones in the feet of the ungulate orders has a

direct relation to the dryness of the ground they inhabit, and the

possibility of speed which their habit permits them or necessarily

imposes on them."[205]

If there is any truth in the explanation here briefly summarised, it

must entirely depend on the fact of individual modifications thus

produced being hereditary, and we yet await the proof of this. In the

meantime it is clear that the very same results could have been brought

about by variation and natural selection. For the toes, like all other

organs, vary in size and proportions, and in their degree of union or

separation; and if in one group of animals it was beneficial to have the

middle toe larger and longer, and in another set to have the two middle

toes of the same size, nothing can be more certain than that these

particular modifications would be continuously preserved, and the very

results we see ultimately produced.

The oft-repeated objections that the cause of variations is unknown,

that there must be something to determine variations in the right

direction; that "natural selection includes no actively progressive

principle, but must wait for the development of variation, and then,

after securing the survival of the best, wait again for the best to

project its own variations for selection," we have already sufficiently

answered by showing that variation--in abundant or typical species--is

always present in ample amount; that it exists in all parts and organs;

that these vary, for the most part, independently, so that any required

combination of variations can be secured; and finally, that all

variation is necessarily either in excess or defect of the mean

condition, and that, consequently, the right or favourable variations

are so frequently present that the unerring power of natural selection

never wants materials to work upon.

\_Supposed Action of Animal Intelligence.\_

The following passage briefly summarises Mr. Cope's position:

"Intelligence is a conservative principle, and will always direct effort

and use into lines which will be beneficial to its possessor. Here we

have the source of the fittest, \_i.e.\_ addition of parts by increase and

location of growth-force, directed by the influence of various kinds of

compulsion in the lower, and intelligent option among higher animals.

Thus intelligent choice, taking advantage of the successive evolution of

physical conditions, may be regarded as the \_originator of the fittest\_,

while natural selection is the tribunal to which all results of

accelerated growth are submitted. This preserves or destroys them, and

determines the new points of departure on which accelerated growth shall

build."[206]

This notion of "intelligence"--the intelligence of the animal

itself--determining its own variation, is so evidently a very partial

theory, inapplicable to the whole vegetable kingdom, and almost so to

all the lower forms of animals, amongst which, nevertheless, there is

the very same adaptation and co-ordination of parts and functions as

among the highest, that it is strange to see it put forward with such

confidence as necessary for the completion of Darwin's theory. If "the

various kinds of compulsion"--by which are apparently meant the laws of

variation, growth, and reproduction, the struggle for existence, and the

actions necessary to preserve life under the conditions of the animal's

environment--are sufficient to have developed the varied forms of the

lower animals and of plants, we can see no reason why the same

"compulsion" should not have carried on the development of the higher

animals also. The action of this "intelligent option" is altogether

unproved; while the acknowledgment that natural selection is the

tribunal which either preserves or destroys the variations submitted to

it, seems quite inconsistent with the statement that intelligent choice

is the "orginator of the fittest," since whatever is really "the

fittest" can never be destroyed by natural selection, which is but

another name for the survival of the fittest. If "the fittest" is always

definitely produced by some other power, then natural selection is not

wanted. If, on the other hand, both fit and unfit are produced, and

natural selection decides between them, that is pure Darwinism, and Mr.

Cope's theories have added nothing to it.

[Illustration: FIG. 35.--Transformation of Artemia salina to A.

Milhausenii; 1, tail-lobe of A. salina, and its transition through

2,3,4,5, to 6, into that of A. Milhausenii; 7, post-abdomen of A.

salina; 8, post-abdomen of a form bred in brackish water; 9, gill of A.

Milhausenii; 10, gill of A. salina. (From Schmankewitsch.)]

\_Semper on the Direct Influence of the Environment.\_

Another eminent naturalist, Professor Karl Semper of WÃ¼rzburg, also

adopts the view of the direct transforming power of the environment, and

has brought together an immense body of interesting facts showing the

influence of food, of light, of temperature, of still water and moving

water, of the atmosphere and its currents, of gravitation, and of other

organisms, in modifying the forms and other characteristics of

animals.[207] He believes that these various influences produce a direct

and important effect, and that this effect is accumulated by

inheritance; yet he acknowledges that we have no direct evidence of

this, and there is hardly a single case adduced in the book which is not

equally well explained by adaptation, brought about by the survival of

beneficial variations. Perhaps the most remarkable case he has brought

forward is that of the transformation of species of crustaceans by a

change in the saltness of the water (see Fig. 35). Artemia salina lives

in brackish water, while A. Milhausenii inhabits water which is much

salter. They differ greatly in the form of the tail-lobes, and in the

presence or absence of spines upon the tail, and had always been

considered perfectly distinct species. Yet either was transformed into

the other in a few generations, during which the saltness of the water

was gradually altered. Yet more, A. salina was gradually accustomed to

fresher water, and in the course of a few generations, when the water

had become perfectly fresh, the species was changed into Branchipus

stagnalis, which had always been considered to belong to a different

genus on account of differences in the form of the antennae and of the

posterior segments of the body (see Fig. 36). This certainly appears to

be a proof of change of conditions producing a change of form

independently of selection, and of that change of form, while remaining

under the same conditions, being inherited. Yet there is this

peculiarity in the case, that there is a chemical change in the water,

and that this water permeates the whole body, and must be absorbed by

the tissues, and thus affect the ova and even the reproductive

elements, and in this way may profoundly modify the whole organisation.

Why and how the external effects are limited to special details of the

structure we do not know; but it does not seem as if any far-reaching

conclusions as to the cumulative effect of external conditions on the

higher terrestrial animals and plants, can be drawn from such an

exceptional phenomenon. It seems rather analogous to those effects of

external influences on the very lowest organisms in which the vegetative

and reproductive organs are hardly differentiated, in which case such

effects are doubtless inherited.[208]

[Illustration: FIG. 36. \_a.\_ Branchipus stagnalis. \_b.\_ Artemia salina.]

\_Professor Geddes's Theory of Variation in Plants.\_

In a paper read before the Edinburgh Botanical Society in 1886 Mr.

Patrick Geddes laid down the outlines of a fundamental theory of plant

variation, which he has further extended in the article "Variation and

Selection" in the \_Encydopaedia Britannica\_, and in a paper read before

the Linnaean Society but not yet published.

A theory of variation should deal alike with the origin of specific

distinctions and with those vaster differences which characterise the

larger groups, and he thinks it should answer such questions as--How an

axis comes to be arrested to form a flower? how the various forms of

inflorescence were evolved? how did perigynous or epigynous flowers

arise from hypogynous flowers? and many others equally fundamental.

Natural selection acting upon numerous accidental variations will not,

he urges, account for such general facts as these, which must depend on

some constant law of variation. This law he believes to be the

well-known antagonism of vegetative and reproductive growth acting

throughout the whole course of plant development; and he uses it to

explain many of the most characteristic features of the structure of

flowers and fruits.

Commencing with the origin of the flower, which all botanists agree in

regarding as a shortened branch, he explains this shortening as an

inevitable physiological fact, since the cost of the development of the

reproductive elements is so great as necessarily to check vegetative

growth. In the same manner the shortening of the inflorescence from

raceme to spike or umbel, and thence to the capitulum or dense

flower-head of the composite plants is brought about. This shortening,

carried still further, produces the flattened leaf-like receptacle of

Dorstenia, and further still the deeply hollowed fruity receptacle of

the fig.

The flower itself undergoes a parallel modification due to a similar

cause. It is formed by a series of modified leaves arranged round a

shortened axis. In its earlier stages the number of these modified

leaves is indefinite, as in many Ranunculaceae; and the axis itself is

not greatly shortened, as in Myosurus. The first advance is to a

definite number of parts and a permanently shortened axis, in the

arrangement termed hypogynous, in which all the whorls are quite

distinct from each other. In the next stage there is a further

shortening of the central axis, leaving the outer portion as a ring on

which the petals are inserted, producing the arrangement termed

perigynous. A still further advance is made by the contraction of the

axis, so as to leave the central part forming the ovary quite below the

flower, which is then termed epigynous.

These several modifications are said to be parallel and definite, and to

be determined by the continuous checking of vegetation by reproduction

along what is an absolute groove of progressive change. This being the

case, the importance of natural selection is greatly diminished. Instead

of selecting and accumulating spontaneous indefinite variations, its

function is to retard them after the stage of maximum utility has been

independently reached. The same simple conception is said to unlock

innumerable problems of vegetable morphology, large and small alike. It

explains the inevitable development of gymnosperm into angiosperm by the

checked vegetative growth of the ovule-bearing leaf or carpel; while

such minor adaptations as the splitting fruit of the geranium or the

cupped stigma of the pansy, can be no longer looked upon as achievements

of natural selection, but must be regarded as naturally traceable to

the vegetative checking of their respective types of leaf organ. Again,

a detailed examination of spiny plants practically excludes the

hypothesis of mammalian selection altogether, and shows spines to arise

as an expression of the diminishing vegetativeness--in fact, the ebbing

vitality of a species.[209]

\_Objections to the Theory.\_

The theory here sketched out is enticing, and at first sight seems

calculated to throw much light on the history of plant development; but

on further consideration, it seems wanting in definiteness, while it is

beset with difficulties at every step. Take first the shortening of the

raceme into the umbel and the capitulum, said to be caused by arrest of

vegetative growth, due to the antagonism of reproduction. If this were

the whole explanation of the phenomenon, we should expect the quantity

of seed to increase as this vegetative growth diminished, since the seed

is the product of the reproductive energy of the plant, and its quantity

the best measure of that energy. But is this the case? The ranunculus

has comparatively few seeds, and the flowers are not numerous; while in

the same order the larkspur and the columbine have far more seeds as

well as more flowers, but there is no shortening of the raceme or

diminution of the foliage, although the flowers are large and complex.

So, the extremely shortened and compressed flower-heads of the

compositae produce comparatively few seeds--one only to each flower;

while the foxglove, with its long spike of showy flowers, produces an

enormous number.

Again, if the shortening of the central axis in the successive stages of

hypogynous, perigynous, and epigynous flowers were an indication of

preponderant reproduction and diminished vegetation, we should find

everywhere some clear indications of this fact. The plants with

hypogynous flowers should, as a rule, have less seed and more vigorous

and abundant foliage than those at the other extreme with epigynous

flowers. But the hypogynous poppies, pinks, and St. John's worts have

abundance of seed and rather scanty foliage; while the epigynous

dogwoods and honeysuckles have few seeds and abundant foliage. If,

instead of the number of the seeds, we take the size of the fruit as an

indication of reproductive energy, we find this at a maximum in the

gourd family, yet their rapid and luxuriant growth shows no diminution

of vegetative power. So that the statement that plant modifications

proceed "along an absolute groove of progressive change" is contradicted

by innumerable facts indicating advance and regression, improvement or

degradation, according as the ever-changing environment renders one form

more advantageous than the other. As one instance I may mention the

Anonaceae or custard-apple tribe, which are certainly an advance from

the Ranunculaceae; yet in the genus Polyalthea the fruit consists of a

number of separate carpels, each borne on a long stalk, as if reverting

to the primitive stalked carpellary leaves.

\_On the Origin of Spines.\_

But perhaps the most extraordinary application of the theory is that

which considers spines to be an indication of the "ebbing vitality of a

species," and which excludes "mammalian selection altogether." If this

were true, spines should occur mainly in feeble, rare, and dying-out

species, instead of which we have the hawthorn, one of our most vigorous

shrubs or trees, with abundant vitality and an extensive range over the

whole Palaearctic region, showing that it is really a dominant species.

In North America the numerous thorny species of Crataegus are equally

vigorous, as are the false acacia (Robinia) and the honey-locust

(Gleditschia). Neither have the numerous species of very spiny Acacias

been noticed to be rarer or less vigorous than the unarmed kinds.

On the other point--that spines are not due to mammalian selection--we

are able to adduce what must be considered direct and conclusive

evidence. For if spines, admittedly produced by aborted branches,

petioles, or peduncles, are due solely or mainly to diminished

vegetativeness or ebbing vitality, they ought to occur in all countries

alike, or at all events in all whose similar conditions tend to check

vegetation; whereas, if they are, solely or mainly, developed as a

protection against the attacks of herbivorous mammals, they ought to be

most abundant where these are plentiful, and rare or absent where

indigenous mammalia are wanting. Oceanic islands, as compared with

continents, would thus furnish a crucial test of the two theories; and

Mr. Hemsley of Kew, who has specially studied insular floras, has given

me some valuable information on this point. He says: "There are no spiny

or prickly plants in the indigenous element of the St. Helena flora. The

relatively rich flora of the Sandwich Isles is not absolutely without a

prickly plant, but almost so. All the endemic genera are unarmed, and

the endemic species of almost every other genus. Even such genera as

Zanthoxylon, Acacia, Xylosoma, Lycium, and Solanum, of which there are

many armed species in other countries, are only represented by unarmed

species. The two endemic Rubi have the prickles reduced to the setaceous

condition, and the two palms are unarmed.

"The flora of the Galapagos includes a number of prickly plants, among

them several cacti (these have not been investigated and may be American

species), but I do not think one of the known endemic species of any

family is prickly or spiny.

"Spiny and prickly plants are also rare in New Zealand, but there are

the formidably armed species of wild Spaniard (Aciphylla), one species

of Rubus, the pungent-leaved Epacrideae and a few others."

Mr. J.G. Baker of Kew, who has specially studied the flora of Mauritius

and the adjacent islands, also writes me on this point. He says: "Taking

Mauritius alone, I do not call to mind a single species that is a

spinose endemic tree or shrub. If you take the whole group of islands

(Mauritius, Bourbon, Seychelles, and Rodriguez), there will be about a

dozen species, but then nine of these are palms. Leaving out palms, the

trees and shrubs of that part of the world are exceptionally

non-spinose."

These are certainly remarkable facts, and quite inexplicable on the

theory of spines being caused solely by checked vegetative growth, due

to weakness of constitution or to an arid soil and climate. For the

Galapagos and many parts of the Sandwich Islands are very arid, as is a

considerable part of the North Island of New Zealand. Yet in our own

moist climate and with our very limited number of trees and shrubs we

have about eighteen spiny or prickly species, more, apparently, than in

the whole endemic floras of the Mauritius, Sandwich Islands, and

Galapagos, though these are all especially rich in shrubby and arboreal

species. In New Zealand the prickly Rubus is a leafless trailing plant,

and its prickles are probably a protection against the large snails of

the country, several of which have shells from two to three and a half

inches long.[210] The "wild Spaniards" are very spiny herbaceous

Umbelliferae, and may have gained their spines to preserve them from

being trodden down or eaten by the Moas, which, for countless ages, took

the place of mammals in New Zealand. The exact use or meaning of the

spines in palms is more doubtful, though they are, no doubt, protective

against some animals; but it is certainly an extraordinary fact that in

the entire flora of the Mauritius, so largely consisting of trees and

shrubs, not a single endemic species should be thorny or spiny.

If now we consider that every continental flora produces a considerable

proportion of spiny and thorny species, and that these rise to a maximum

in South Africa, where herbivorous mammalia were (before the settlement

of the country), perhaps, more abundant and varied than in any other

part of the world; while another district, remarkable for well-armed

vegetation, is Chile, where the camel-like vicugnas, llamas, and

alpacas, and an abundance of large rodents wage perpetual war against

shrubby vegetation, we shall see the full significance of the almost

total absence of thorny and spiny plants in the chief oceanic islands;

and so far from "excluding the hypothesis of mammalian selection

altogether," we shall find in this hypothesis the only satisfactory

explanation of the facts.

From the brief consideration of Professor Geddes's theory now given, we

conclude that, although the antagonism between vegetative and

reproductive growth is a real agency, and must be taken account of in

our endeavour to explain many of the fundamental facts in the structure

and form of plants, yet it is so overpowered and directed at every step

by the natural selection of favourable variations, that the results of

its exclusive and unmodified action are nowhere to be found in nature.

It may be allowed to rank as one of those "laws of growth," of which so

many have now been indicated, and which were always recognised by Darwin

as underlying all variation; but unless we bear in mind that its action

must always be subordinated to natural selection, and that it is

continually checked, or diverted, or even reversed by the necessity of

adaptation to the environment, we shall be liable to fall into such

glaring errors as the imputing to "ebbing vitality" alone such a

widespread phenomenon as the occurrence of spines and thorns, while

ignoring altogether the influence of the organic environment in their

production.[211]

The sketch now given of the chief attempts that have been made to prove

that either the direct action of the environment or certain fundamental

laws of variation are independent causes of modification of species,

shows us that their authors have, in every case, failed to establish

their contention. Any direct action of the environment, or any

characters acquired by use or disuse, can have no effect whatever upon

the race unless they are inherited; and that they are inherited in any

case, except when they directly affect the reproductive cells, has not

been proved. On the other hand, as we shall presently show, there is

much reason for believing that such acquired characters are in their

nature non-heritable.

\_Variation and Selection Overpower the Effects of Use and Disuse.\_

But there is another objection to this theory arising from the very

nature of the effects produced. In each generation the effects of use or

disuse, or of effort, will certainly be very small, while of this small

effect it is not maintained that the whole will be always inherited by

the next generation. How small the effect is we have no means of

determining, except in the case of disuse, which Mr. Darwin investigated

carefully. He found that in twelve fancy breeds of pigeons, which are

often kept in aviaries, or if free fly but little, the sternum had been

reduced by about one-seventh or one-eighth of its entire length, and

that of the scapula about one-ninth. In domestic ducks the weight of the

wing-bones in proportion to that of the whole skeleton had decreased

about one-tenth. In domestic rabbits the bones of the legs were found to

have increased in weight in due proportion to the increased weight of

the body, but those of the hind legs were rather less in proportion to

those of the fore legs than in the wild animal, a difference which may

be imputed to their being less used in rapid motion. The pigeons,

therefore, afford the greatest amount of reduction by

disuse--one-seventh of the length of the sternum. But the pigeon has

certainly been domesticated four or five thousand years; and if the

reduction of the wings by disuse has only been going on for the last

thousand years, the amount of reduction in each generation would be

absolutely imperceptible, and quite within the limits of the reduction

due to the absence of selection, as already explained. But, as we have

seen in Chapter III, the fortuitous variation of every part or organ

usually amounts to one-tenth, and often to one-sixth of the average

dimensions--that is, the fortuitous variation in one generation among a

limited number of the individuals of a species is as great as the

cumulative effects of disuse in a thousand generations! If we assume

that the effects of use or of effort in the individual are equal to the

effects of disuse, or even ten or a hundred times greater, they will

even then not equal, in each generation, the amount of the fortuitous

variations of the same part. If it be urged that the effects of use

would modify all the individuals of a species, while the fortuitous

variations to the amount named only apply to a portion of them, it may

be replied, that that portion is sufficiently large to afford ample

materials for selection, since it often equals the numbers that can

annually survive; while the recurrence in each successive generation of

a like amount of variation would render possible such a rapid adjustment

to new conditions that the effects of use or disuse would be as nothing

in comparison. It follows, that even admitting the modifying effects of

the environment, and that such modifications are inherited, they would

yet be entirely swamped by the greater effects of fortuitous variation,

and the far more rapid cumulative results of the selection of such

variations.

\_Supposed Action of the Environment in Initiating Variations.\_

It is, however, urged that the reaction of the environment initiates

variations, which without it would never arise; such, for instance, as

the origin of horns through the pressures and irritations caused by

butting, or otherwise using the head as a weapon or for defence.

Admitting, for the sake of argument, that this is so, all the evidence

we possess shows that, from the very first appearance of the rudiment of

such an organ, it would vary to a greater extent than the amount of

growth directly produced by use; and these variations would be subject

to selection, and would thus modify the organ in ways which use alone

would never bring about. We have seen that this has been the case with

the branching antlers of the stag, which have been modified by

selection, so as to become useful in other ways than as a mere weapon;

and the same has almost certainly been the case with the variously

curved and twisted horns of antelopes. In like manner, every conceivable

rudiment would, from its first appearance, be subject to the law of

variation and selection, to which, thenceforth, the direct effect of the

environment would be altogether subordinate.

A very similar mode of reasoning will apply to the other branch of the

subject--the initiation of structures and organs by the action of the

fundamental laws of growth. Admitting that such laws have determined

some of the main divisions of the animal and vegetable kingdom, have

originated certain important organs, and have been the fundamental cause

of certain lines of development, yet at every step of the process these

laws must have acted in entire subordination to the law of natural

selection. No modification thus initiated could have advanced a single

step, unless it were, on the whole, a useful modification; while its

entire future course would be necessarily subject to the laws of

variation and selection, by which it would be sometimes checked,

sometimes hastened on, sometimes diverted to one purpose, sometimes to

another, according as the needs of the organism, under the special

conditions of its existence, required such modification. We need not

deny that such laws and influences may have acted in the manner

suggested, but what we do deny is that they could possibly escape from

the ever-present and all-powerful modifying effects of variation and

natural selection.[212]

\_Weismann's Theory of Heredity.\_

Professor August Weismann has put forth a new theory of heredity founded

upon the "continuity of the germ-plasm," one of the logical consequences

of which is, that acquired characters of whatever kind are not

transmitted from parent to offspring. As this is a matter of vital

importance to the theory of natural selection, and as, if well founded,

it strikes away the foundations of most of the theories discussed in the

present chapter, a brief outline of Weismann's views must be attempted,

although it is very difficult to make them intelligible to persons

unfamiliar with the main facts of modern embryology.[213]

The problem is thus stated by Weismann: "How is it that in the case of

all higher animals and plants a single cell is able to separate itself

from amongst the millions of most various kinds of which an organism is

composed, and by division and complicated differentiation to reconstruct

a new individual with marvellous likeness, unchanged in many cases even

throughout whole geological periods?" Darwin attempted to solve the

problem by his theory of "Pangenesis," which supposed that every

individual cell in the body gave off gemmules or germs capable of

reproducing themselves, and that portions of these germs of each of the

almost infinite number of cells permeate the whole body and become

collected in the generative cells, and are thus able to reproduce the

whole organism. This theory is felt to be so ponderously complex and

difficult that it has met with no general acceptance among

physiologists.

The fact that the germ-cells \_do\_ reproduce with wonderful accuracy not

only the general characters of the species, but many of the individual

characteristics of the parents or more remote ancestors, and that this

process is continued from generation to generation, can be accounted

for, Weismann thinks, only on two suppositions which are physiologically

possible. Either the substance of the parent germ-cell, after passing

through a cycle of changes required for the construction of a new

individual, possesses the capability of producing anew germ-cells

identical with those from which that individual was developed, or \_the

new germ-cells arise, as far as their essential and characteristic

substance is concerned, not at all out of the body of the individual,

but direct from the parent germ-cell\_. This latter view Weismann holds

to be the correct one, and, on this theory, heredity depends on the fact

that a substance of special molecular composition passes over from one

generation to another. This is the "germ-plasm," the power of which to

develop itself into a perfect organism depends on the extraordinary

complication of its minutest structure. At every new birth a portion of

the specific germ-plasm, which the parent egg-cell contains, is not used

up in producing the offspring, but is reserved unchanged to produce the

germ-cells of the following generation. Thus the germ-cells--so far as

regards their essential part the germ-plasm--are not a product of the

body itself, but are related to one another in the same way as are a

series of generations of unicellular organisms derived from one another

by a continuous course of simple division. Thus the question of heredity

is reduced to one of growth. A minute portion of the very same

germ-plasm from which, first the germ-cell, and then the whole organism

of the parent, were developed, becomes the starting-point of the growth

of the child.

\_The Cause of Variation.\_

But if this were all, the offspring would reproduce the parent exactly,

in every detail of form and structure; and here we see the importance of

sex, for each new germ grows out of the united germ-plasms of two

parents, whence arises a mingling of their characters in the offspring.

This occurs in each generation; hence every individual is a complex

result reproducing in ever-varying degrees the diverse characteristics

of his two parents, four grandparents, eight great-grandparents, and

other more remote ancestors; and that ever-present individual variation

arises which furnishes the material for natural selection to act upon.

Diversity of sex becomes, therefore, of primary importance as \_the cause

of variation\_. Where asexual generation prevails, the characteristics of

the individual alone are reproduced, and there are thus no means of

effecting the change of form or structure required by changed conditions

of existence. Under such changed conditions a complex organism, if only

asexually propagated, would become extinct. But when a complex organism

is sexually propagated, there is an ever-present cause of change which,

though slight in any one generation, is cumulative, and under the

influence of selection is sufficient to keep up the harmony between the

organism and its slowly changing environment.[214]

\_The Non-Heredity of Acquired Characters.\_

Certain observations on the embryology of the lower animals are held to

afford direct proof of this theory of heredity, but they are too

technical to be made clear to ordinary readers. A logical result of the

theory is the impossibility of the transmission of acquired characters,

since the molecular structure of the germ-plasm is already determined

within the embryo; and Weismann holds that there are no facts which

really prove that acquired characters can be inherited, although their

inheritance has, by most writers, been considered so probable as hardly

to stand in need of direct proof.

We have already shown, in the earlier part of this chapter, that many

instances of change, imputed to the inheritance of acquired variations,

are really cases of selection; while the very fact that \_use\_ implies

\_usefulness\_ renders it almost impossible to eliminate the action of

selection in a state of nature. As regards mutilations, it is generally

admitted that they are not hereditary, and there is ample evidence on

this point. When it was the fashion to dock horses' tails, it was not

found that horses were born with short tails; nor are Chinese women born

with distorted feet; nor are any of the numerous forms of racial

mutilation in man, which have in some cases been carried on for hundreds

of generations, inherited. Nevertheless, a few cases of apparent

inheritance of mutilations have been recorded,[215] and these, if

trustworthy, are difficulties in the way of the theory. The undoubted

inheritance of disease is hardly a difficulty, because the

predisposition to disease is a congenital, not an acquired character,

and as such would be the subject of inheritance. The often-quoted case

of a disease induced by mutilation being inherited (Brown-Sequard's

epileptic guinea-pigs) has been discussed by Professor Weismann, and

shown to be not conclusive. The mutilation itself--a section of certain

nerves--was never inherited, but the resulting epilepsy, or a general

state of weakness, deformity, or sores, was sometimes inherited. It is,

however, possible that the mere injury introduced and encouraged the

growth of certain microbes, which, spreading through the organism,

sometimes reached the germ-cells, and thus transmitted a diseased

condition to the offspring. Such a transference of microbes is believed

to occur in syphilis and tuberculosis, and has been ascertained to occur

in the case of the muscardine silkworm disease.[216]

\_The Theory of Instinct.\_

The theory now briefly outlined cannot be said to be proved, but it

commends itself to many physiologists as being inherently probable, and

as furnishing a good working hypothesis till displaced by a better. We

cannot, therefore, accept any arguments against the agency of natural

selection which are based upon the opposite and equally unproved theory

that acquired characters are inherited; and as this applies to the whole

school of what may be termed Neo-Lamarckians, their speculations cease

to have any weight.

The same remark applies to the popular theory of instincts as being

inherited habits; though Darwin gave very little weight to this, but

derived almost all instincts from spontaneous useful variations which,

like other spontaneous variations, are of course inherited. At first

sight it appears as if the acquired habits of our trained

dogs--pointers, retrievers, etc.--are certainly inherited; but this need

not be the case, because there must be some structural or psychical

peculiarities, such as modifications in the attachments of muscles,

increased delicacy of smell or sight, or peculiar likes and dislikes,

which are inherited; and from these, peculiar habits follow as a natural

consequence, or are easily acquired. Now, as selection has been

constantly at work in improving all our domestic animals, we have

unconsciously modified the structure, while preserving only those

animals which best served our purpose in their peculiar faculties,

instincts, or habits.

Much of the mystery of instinct arises from the persistent refusal to

recognise the agency of imitation, memory, observation, and reason as

often forming part of it. Yet there is ample evidence that such agency

must be taken into account. Both Wilson and Leroy state that young birds

build inferior nests to old ones, and the latter author observes that

the best nests are made by birds whose young remain longest in the nest.

So, migration is now well ascertained to be effected by means of vision,

long flights being made on bright moonlight nights when the birds fly

very high, while on cloudy nights they fly low, and then often lose

their way. Thousands annually fly out to sea and perish, showing that

the instinct to migrate is imperfect, and is not a good substitute for

reason and observation.

Again, much of the perfection of instinct is due to the extreme severity

of the selection during its development, any failure involving

destruction. The chick which cannot break the eggshell, the caterpillar

that fails to suspend itself properly or to spin a safe cocoon, the bees

that lose their way or that fail to store honey, inevitably perish. So

the birds that fail to feed and protect their young, or the butterflies

that lay their eggs on the wrong food-plant, leave no offspring, and the

race with imperfect instincts perishes. Now, during the long and very

slow course of development of each organism, this rigid selection at

every step of progress has led to the preservation of every detail of

structure, faculty, or habit that has been necessary for the

preservation of the race, and has thus gradually built up the various

instincts which seem so marvellous to us, but which can yet be shown to

be in many cases still imperfect. Here, as everywhere else in nature, we

find comparative, not absolute perfection, with every gradation from

what is clearly due to imitation or reason up to what seems to us

perfect instinct--that in which a complex action is performed without

any previous experience or instruction.[217]

\_Concluding Remarks.\_

Having now passed in review the more important of the recent objections

to, or criticisms of, the theory of natural selection, we have arrived

at the conclusion that in no one case have the writers in question been

able materially to diminish its importance, or to show that any of the

laws or forces to which they appeal can act otherwise than in strict

subordination to it. The direct action of the environment as set forth

by Mr. Herbert Spencer, Dr. Cope, and Dr. Karl Semper, even if we admit

that its effects on the individual are transmitted by inheritance, are

so small in comparison with the amount of spontaneous variation of every

part of the organism that they must be quite overshadowed by the latter.

And if such direct action may, in some cases, have initiated certain

organs or outgrowths, these must from their very first beginnings have

been subject to variation and natural selection, and their further

development have been almost wholly due to these ever-present and

powerful causes. The same remark applies to the views of Professor

Geddes on the laws of growth which have determined certain essential

features in the morphology of plants and animals. The attempt to

substitute these laws for those of variation and natural selection has

failed in cases where we can apply a definite test, as in that of the

origin of spines on trees and shrubs; while the extreme diversity of

vegetable structure and form among the plants of the same country and of

the same natural order, of itself affords a proof of the preponderating

influence of variation and natural selection in keeping the many diverse

forms in harmony with the highly complex and ever-changing environment.

Lastly, we have seen that Professor Weismann's theory of the continuity

of the germ-plasm and the consequent non-heredity of acquired

characters, while in perfect harmony with all the well-ascertained facts

of heredity and development, adds greatly to the importance of natural

selection as the one invariable and ever-present factor in all organic

change, and that which can alone have produced the temporary fixity

combined with the secular modification of species. While admitting, as

Darwin always admitted, the co-operation of the fundamental laws of

growth and variation, of correlation and heredity, in determining the

direction of lines of variation or in the initiation of peculiar organs,

we find that variation and natural selection are ever-present agencies,

which take possession, as it were, of every minute change originated by

these fundamental causes, check or favour their further development, or

modify them in countless varied ways according to the varying needs of

the organism. Whatever other causes have been at work, Natural Selection

is supreme, to an extent which even Darwin himself hesitated to claim

for it. The more we study it the more we are convinced of its

overpowering importance, and the more confidently we claim, in Darwin's

own words, that it "has been the most important, but not the exclusive,

means of modification."

FOOTNOTES:

[Footnote 198: See the Duke of Argyll's letter in \_Nature\_, vol. xxxiv.

p. 336.]

[Footnote 199: \_Journal of the Anthropological Institute,\_ vol. xv. pp.

246-260.]

[Footnote 200: The idea of the non-heredity of acquired variations was

suggested by the summary of Professor Weismann's views, in \_Nature\_,

referred to later on. But since this chapter was written I have, through

the kindness of Mr. E.B. Poulton, seen some of the proofs of the

forthcoming translation of Weismann's Essays on Heredity, in which he

sets forth an explanation very similar to that here given. On the

difficult question of the almost entire disappearance of organs, as in

the limbs of snakes and of some lizards, he adduces "a certain form of

correlation, which Roux calls 'the struggle of the parts in the

organism,'" as playing an important part. Atrophy following disuse is

nearly always attended by the corresponding increase of other organs:

blind animals possess more developed organs of touch, hearing, and

smell; the loss of power in the wings is accompanied by increased

strength of the legs, etc. Now as these latter characters, being useful,

will be selected, it is easy to understand that a congenital increase of

these will be accompanied by a corresponding congenital diminution of

the unused organ; and in cases where the means of nutrition are

deficient, every diminution of these useless parts will be a gain to the

whole organism, and thus their complete disappearance will, in some

cases, be brought about directly by natural selection. This corresponds

with what we know of these rudimentary organs.

It must, however, be pointed out that the non-heredity of acquired

characters was maintained by Mr. Francis Galton more than twelve years

ago, on theoretical considerations almost identical with those urged by

Professor Weismann; while the insufficiency of the evidence for their

hereditary transmission was shown, by similar arguments to those used

above and in the work of Professor Weismann already referred to (see "A

Theory of Heredity," in \_Journ. Anthrop. Instit.\_, vol. v. pp.

343-345).]

[Footnote 201: This explanation is derived from Weismann's Theory of the

Continuity of the Germ-Plasm as summarised in \_Nature\_.]

[Footnote 202: See a collection of his essays under the title, \_The

Origin of the Fittest: Essays on Evolution\_, D. Appleton and Co. New

York. 1887.]

[Footnote 203: \_Origin of the Fittest\_, p. 174.]

[Footnote 204: \_Ibid.\_ p. 29. It may be here noted that Darwin found

these theories unintelligible. In a letter to Professor E.T. Morse in

1877, he writes: "There is one point which I regret you did not make

clear in your Address, namely, what is the meaning and importance of

Professors Cope and Hyatt's views on acceleration and retardation? I

have endeavoured, and given up in despair, the attempt to grasp their

meaning" (\_Life and Letters\_, vol. iii. p. 233).]

[Footnote 205: \_Origin of the Fittest\_, p. 374.]

[Footnote 206: \_Origin of the Fittest\_, p. 40.]

[Footnote 207: \_The Natural Conditions of Existence as they Affect

Animal Life.\_ London, 1883.]

[Footnote 208: In Dr. Weismann's essay on "Heredity," already referred

to, he considers it not improbable that changes in organisms produced by

climatic influences may be inherited, because, as these changes do not

affect the external parts of an organism only, but often, as in the case

of warmth or moisture permeate the whole structure, they may possibly

modify the germ-plasm itself, and thus induce variations in the next

generation. In this way, he thinks, may possibly be explained the

climatic varieties of certain butterflies, and some other changes which

seem to be effected by change of climate in a few generations.]

[Footnote 209: This brief indication of Professor Geddes's views is

taken from the article "Variation and Selection" in the \_Encyclopedia

Britannica\_, and a paper "On the Nature and Causes of Variation in

Plants" in \_Trans. and Proc. of the Edinburgh Botanical Society\_, 1886;

and is, for the most part, expressed in his own words.]

[Footnote 210: Placostylis bovinus, 3Â½ inches long; Paryphanta Busbyi, 3

in. diam.; P. Hochstetteri, 2Â¾ in. diam.]

[Footnote 211: The general arguments and objections here set forth will

apply with equal force to Professor G. Henslow's theory of the origin of

the various forms and structures of flowers as due to "the responsive

actions of the protoplasm in consequence of the irritations set up by

the weights, pressures, thrusts, tensions, etc., of the insect visitors"

(\_The Origin of Floral Structures through Insect and other Agencies\_, p.

340). On the assumption that acquired characters are inherited, such

irritations may have had something to do with the initiation of

variations and with the production of certain details of structure, but

they are clearly incompetent to have brought about the more important

structural and functional modifications of flowers. Such are, the

various adjustments of length and position of the stamens to bring the

pollen to the insect and from the insect to the stigma; the various

motions of stamens and styles at the right time and the right direction;

the physiological adjustments bringing about fertility or sterility in

heterostyled plants; the traps, springs, and complex movements of

various parts of orchids; and innumerable other remarkable phenomena.

For the explanation of these we have no resource but variation and

selection, to the effects of which, acting alternately with regression

or degradation as above explained (p. 328) must be imputed the

development of the countless floral structures we now behold. Even the

primitive flowers, whose initiation may, perhaps, have been caused, or

rendered possible, by the irritation set up by insects' visits, must,

from their very origin, have been modified, in accordance with the

supreme law of utility, by means of variation and survival of the

fittest.]

[Footnote 212: In an essay on "The Duration of Life," forming part of

the translation of Dr. Weismann's papers already referred to, the author

still further extends the sphere of natural selection by showing that

the average duration of life in each species has been determined by it.

A certain length of life is essential in order that the species may

produce offspring sufficient to ensure its continuance under the most

unfavourable conditions; and it is shown that the remarkable

inequalities of longevity in different species and groups may be thus

accounted for. Yet more, the occurrence of death in the higher

organisms, in place of the continued survival of the unicellular

organisms however much they may increase by subdivision, may be traced

to the same great law of utility for the race and survival of the

fittest. The whole essay is of exceeding interest, and will repay a

careful perusal. A similar idea occurred to the present writer about

twenty years back, and was briefly noted down at the time, but

subsequently forgotten.]

[Footnote 213: The outline here given is derived from two articles in

\_Nature\_, vol. xxxiii. p. 154, and vol. xxxiv. p. 629, in which

Weismann's papers are summarised and partly translated.]

[Footnote 214: There are many indications that this explanation of the

cause of variation is the true one. Mr. E.B. Poulton suggests one, in

the fact that parthenogenetic reproduction only occurs in isolated

species, not in groups of related species; as this shows that

parthenogenesis cannot lead to the evolution of new forms. Again, in

parthenogenetic females the complete apparatus for fertilisation remains

unreduced; but if these varied as do sexually produced animals, the

organs referred to, being unused, would become rudimentary.

Even more important is the significance of the "polar bodies," as

explained by Weismann in one of his \_Essays\_; since, if his

interpretation of them be correct, variability is a necessary

consequence of sexual generation.]

[Footnote 215: Darwin's \_Animals and Plants\_, vol. ii. pp. 23, 24.]

[Footnote 216: In his essay on "Heredity," Dr. Weismann discusses many

other cases of supposed inheritance of acquired characters, and shows

that they can all be explained in other ways. Shortsightedness among

civilised nations, for example, is due partly to the absence of

selection and consequent regression towards a mean, and partly to its

individual production by constant reading.]

[Footnote 217: Weismann explains instinct on similar lines, and gives

many interesting illustrations (see \_Essays on Heredity\_). He holds

"that all instinct is entirely due to the operation of natural

selection, and has its foundation, not upon inherited experiences, but

upon variations of the germ." Many interesting and difficult cases of

instinct are discussed by Darwin in Chapter VIII of the \_Origin of

Species\_, which should be read in connection with the above remarks.

Since this chapter was written my attention has been directed to Mr.

Francis Galton's \_Theory of Heredity\_ (already referred to at p. 417)

which was published thirteen years ago as an alternative for Darwin's

theory of pangenesis.

Mr. Galton's theory, although it attracted little attention, appears to

me to be substantially the same as that of Professor Weismann. Galton's

"stirp" is Weismann's "germ-plasm." Galton supposes the sexual elements

in the offspring to be directly formed from the residue of the \_stirp\_

not used up in the development of the body of the parent--Weismann's

"continuity of the germ-plasm." Galton also draws many of the same

conclusions from his theory. He maintains that characters acquired by

the individual as the result of external influences cannot be inherited,

unless such influences act directly on the reproductive

elements--instancing the possible heredity of alcoholism, because the

alcohol permeates the tissues and may reach the sexual elements. He

discusses the supposed heredity of effects produced by use or disuse,

and explains them much in the same manner as does Weismann. Galton is an

anthropologist, and applies the theory, mainly, to explain the

peculiarities of hereditary transmission in man, many of which

peculiarities he discusses and elucidates. Weismann is a biologist, and

is mostly concerned with the application of the theory to explain

variation and instinct, and to the further development of the theory of

evolution. He has worked it out more thoroughly, and has adduced

embryological evidence in its support; but the views of both writers are

substantially the same, and their theories were arrived at quite

independently. The names of Galton and Weismann should therefore be

associated as discoverers of what may be considered (if finally

established) the most important contribution to the evolution theory

since the appearance of the \_Origin of Species\_.]

CHAPTER XV

DARWINISM APPLIED TO MAN

General identity of human and animal structure--Rudiments and

variations showing relation of man to other mammals--The

embryonic development of man and other mammalia--Diseases common

to man and the lower animals--The animals most nearly allied to

man--The brains of man and apes--External differences of man and

apes--Summary of the animal characteristics of man--The

geological antiquity of man--The probable birthplace of man--The

origin of the moral and intellectual nature of man--The argument

from continuity--The origin of the mathematical faculty--The

origin of the musical and artistic faculties--Independent proof

that these faculties have not been developed by natural

selection--The interpretation of the facts--Concluding remarks.

Our review of modern Darwinism might fitly have terminated with the

preceding chapter; but the immense interest that attaches to the origin

of the human race, and the amount of misconception which prevails

regarding the essential teachings of Darwin's theory on this question,

as well as regarding my own special views upon it, induce me to devote a

final chapter to its discussion.

To any one who considers the structure of man's body, even in the most

superficial manner, it must be evident that it is the body of an animal,

differing greatly, it is true, from the bodies of all other animals, but

agreeing with them in all essential features. The bony structure of man

classes him as a vertebrate; the mode of suckling his young classes him

as a mammal; his blood, his muscles, and his nerves, the structure of

his heart with its veins and arteries, his lungs and his whole

respiratory and circulatory systems, all closely correspond to those of

other mammals, and are often almost identical with them. He possesses

the same number of limbs terminating in the same number of digits as

belong fundamentally to the mammalian class. His senses are identical

with theirs, and his organs of sense are the same in number and occupy

the same relative position. Every detail of structure which is common to

the mammalia as a class is found also in man, while he only differs from

them in such ways and degrees as the various species or groups of

mammals differ from each other. If, then, we have good reason to believe

that every existing group of mammalia has descended from some common

ancestral form--as we saw to be so completely demonstrated in the case

of the horse tribe,--and that each family, each order, and even the

whole class must similarly have descended from some much more ancient

and more generalised type, it would be in the highest degree

improbable--so improbable as to be almost inconceivable--that man,

agreeing with them so closely in every detail of his structure, should

have had some quite distinct mode of origin. Let us, then, see what

other evidence bears upon the question, and whether it is sufficient to

convert the probability of his animal origin into a practical certainty.

\_Rudiments and Variations as Indicating the Relation of Man to other

Mammals.\_

All the higher animals present rudiments of organs which, though useless

to them, are useful in some allied group, and are believed to have

descended from a common ancestor in which they were useful. Thus there

are in ruminants rudiments of incisor teeth which, in some species,

never cut through the gums; many lizards have external rudimentary legs;

while many birds, as the Apteryx, have quite rudimentary wings. Now man

possesses similar rudiments, sometimes constantly, sometimes only

occasionally present, which serve intimately to connect his bodily

structure with that of the lower animals. Many animals, for example,

have a special muscle for moving or twitching the skin. In man there are

remnants of this in certain parts of the body, especially in the

forehead, enabling us to raise our eyebrows; but some persons have it in

other parts. A few persons are able to move the whole scalp so as to

throw off any object placed on the head, and this property has been

proved, in one case, to be inherited. In the outer fold of the ear there

is sometimes a projecting point, corresponding in position to the

pointed ear of many animals, and believed to be a rudiment of it. In the

alimentary canal there is a rudiment--the vermiform appendage of the

caecum--which is not only useless, but is sometimes a cause of disease

and death in man; yet in many vegetable feeding animals it is very long,

and even in the orang-utan it is of considerable length and convoluted.

So, man possesses rudimentary bones of a tail concealed beneath the

skin, and, in some rare cases, this forms a minute external tail.

The variability of every part of man's structure is very great, and many

of these variations tend to approximate towards the structure of other

animals. The courses of the arteries are eminently variable, so that for

surgical purposes it has been necessary to determine the probable

proportion of each variation. The muscles are so variable that in fifty

cases the muscles of the foot were found to be not strictly alike in any

two, and in some the deviations were considerable; while in thirty-six

subjects Mr. J. Wood observed no fewer than 558 muscular variations. The

same author states that in a single male subject there were no fewer

than seven muscular variations, all of which plainly represented muscles

proper to various kinds of apes. The muscles of the hands and

arms--parts which are so eminently characteristic of man--are extremely

liable to vary, so as to resemble the corresponding muscles of the lower

animals. That such variations are due to reversion to a former state of

existence Mr. Darwin thinks highly probable, and he adds: "It is quite

incredible that a man should, through mere accident, abnormally resemble

certain apes in no less than seven of his muscles, if there had been no

genetic connection between them. On the other hand, if man is descended

from some ape-like creature, no valid reason can be assigned why certain

muscles should not suddenly reappear after an interval of many thousand

generations, in the same manner as, with horses, asses, and mules, dark

coloured stripes suddenly reappear on the legs and shoulders, after an

interval of hundreds, or more probably of thousands of

generations."[218]

\_The Embryonic Development of Man and other Mammalia.\_

The progressive development of any vertebrate from the ovum or minute

embryonic egg affords one of the most marvellous chapters in Natural

History. We see the contents of the ovum undergoing numerous definite

changes, its interior dividing and subdividing till it consists of a

mass of cells, then a groove appears marking out the median line or

vertebral column of the future animal, and thereafter are slowly

developed the various essential organs of the body. After describing in

some detail what takes place in the case of the ovum of the dog,

Professor Huxley continues: "The history of the development of any other

vertebrate animal, lizard, snake, frog, or fish tells the same story.

There is always to begin with, an egg having the same essential

structure as that of the dog; the yelk of that egg undergoes division or

segmentation, as it is called, the ultimate products of that

segmentation constitute the building materials for the body of the young

animal; and this is built up round a primitive groove, in the floor of

which a notochord is developed. Furthermore, there is a period in which

the young of all these animals resemble one another, not merely in

outward form, but in all essentials of structure, so closely, that the

differences between them are inconsiderable, while in their subsequent

course they diverge more and more widely from one another. And it is a

general law that the more closely any animals resemble one another in

adult structure, the larger and the more intimately do their embryos

resemble one another; so that, for example, the embryos of a snake and

of a lizard remain like one another longer than do those of a snake and

a bird; and the embryos of a dog and of a cat remain like one another

for a far longer period than do those of a dog and a bird, or of a dog

and an opossum, or even than those of a dog and a monkey."[219]

We thus see that the study of development affords a test of affinity in

animals that are externally very much unlike each other; and we

naturally ask how this applies to man. Is he developed in a different

way from other mammals, as we should certainly expect if he has had a

distinct and altogether different origin? "The reply," says Professor

Huxley, "is not doubtful for a moment. Without question, the mode of

origin and the early stages of the development of man are identical with

those of the animals immediately below him in the scale." And again he

tells us: "It is very long before the body of the young human being can

be readily discriminated from that of the young puppy; but at a

tolerably early period the two become distinguishable by the different

forms of their adjuncts, the yelk-sac and the allantois;" and after

describing these differences he continues: "But exactly in those

respects in which the developing man differs from the dog, he resembles

the ape.... So that it is only quite in the latter stages of development

that the young human being presents marked differences from the young

ape, while the latter departs as much from the dog in its development as

the man does. Startling as this last assertion may appear to be, it is

demonstrably true, and it alone appears to me sufficient to place beyond

all doubt the structural unity of man with the rest of the animal world,

and more particularly and closely with the apes."[220]

A few of the curious details in which man passes through stages common

to the lower animals may be mentioned. At one stage the os coccyx

projects like a true tail, extending considerably beyond the rudimentary

legs. In the seventh month the convolutions of the brain resemble those

of an adult baboon. The great toe, so characteristic of man, forming the

fulcrum which most assists him in standing erect, in an early stage of

the embryo is much shorter than the other toes, and instead of being

parallel with them, projects at an angle from the side of the foot, thus

corresponding with its permanent condition in the quadrumana. Numerous

other examples might be quoted, all illustrating the same general law.

\_Diseases Common to Man and the Lower Animals.\_

Though the fact is so well known, it is certainly one of profound

significance that many animal diseases can be communicated to man, since

it shows similarity, if not identity, in the minute structure of the

tissues, the nature of the blood, the nerves, and the brain. Such

diseases as hydrophobia, variola, the glanders, cholera, herpes, etc.,

can be transmitted from animals to man or the reverse; while monkeys are

liable to many of the same non-contagious diseases as we are. Rengger,

who carefully observed the common monkey (Cebus Azarae) in Paraguay,

found it liable to catarrh, with the usual symptoms, terminating

sometimes in consumption. These monkeys also suffered from apoplexy,

inflammation of the bowels, and cataract in the eye. Medicines produced

the same effect upon them as upon us. Many kinds of monkeys have a

strong taste for tea, coffee, spirits, and even tobacco. These facts

show the similarity of the nerves of taste in monkeys and in ourselves,

and that their whole nervous system is affected in a similar way. Even

the parasites, both external and internal, that affect man are not

altogether peculiar to him, but belong to the same families or genera as

those which infest animals, and in one case, scabies, even the same

species.[221] These curious facts seem quite inconsistent with the idea

that man's bodily structure and nature are altogether distinct from

those of animals, and have had a different origin; while the facts are

just what we should expect if he has been produced by descent with

modification from some common ancestor.

\_The Animals most nearly Allied to Man.\_

By universal consent we see in the monkey tribe a caricature of

humanity. Their faces, their hands, their actions and expressions

present ludicrous resemblances to our own. But there is one group of

this great tribe in which this resemblance is greatest, and they have

hence been called the anthropoid or man-like apes. These are few in

number, and inhabit only the equatorial regions of Africa and Asia,

countries where the climate is most uniform, the forests densest, and

the supply of fruit abundant throughout the year. These animals are now

comparatively well known, consisting of the orang-utan of Borneo and

Sumatra, the chimpanzee and the gorilla of West Africa, and the group of

gibbons or long-armed apes, consisting of many species and inhabiting

South-Eastern Asia and the larger Malay Islands. These last are far

less like man than the other three, one or other of which has at various

times been claimed to be the most man-like of the apes and our nearest

relations in the animal kingdom. The question of the degree of

resemblance of these animals to ourselves is one of great interest,

leading, as it does, to some important conclusions as to our origin and

geological antiquity, and we will therefore briefly consider it.

If we compare the skeletons of the orang or chimpanzee with that of man,

we find them to be a kind of distorted copy, every bone corresponding

(with very few exceptions), but altered somewhat in size, proportions,

and position. So great is this resemblance that it led Professor Owen to

remark: "I cannot shut my eyes to the significance of that all-pervading

similitude of structure--every tooth, every bone, strictly

homologous--which makes the determination of the difference between

\_Homo\_ and \_Pithecus\_ the anatomist's difficulty."

The actual differences in the skeletons of these apes and that of

man--that is, differences dependent on the presence or absence of

certain bones, and not on their form or position--have been enumerated

by Mr. Mivart as follows:--(1) In the breast-bone consisting of but two

bones, man agrees with the gibbons; the chimpanzee and gorilla having

this part consisting of seven bones in a single series, while in the

orang they are arranged in a double series of ten bones. (2) The normal

number of the ribs in the orang and some gibbons is twelve pairs, as in

man, while in the chimpanzee and gorilla there are thirteen pairs. (3)

The orang and the gibbons also agree with man in having five lumbar

vertebrae, while in the gorilla and the chimpanzee there are but four,

and sometimes only three. (4) The gorilla and chimpanzee agree with man

in having eight small bones in the wrist, while the orang and the

gibbons, as well as all other monkeys, have nine.[222]

The differences in the form, size, and attachments of the various bones,

muscles, and other organs of these apes and man are very numerous and

exceedingly complex, sometimes one species, sometimes another agreeing

most nearly with ourselves, thus presenting a tangled web of affinities

which it is very difficult to unravel. Estimated by the skeleton alone,

the chimpanzee and gorilla seem nearer to man than the orang, which last

is also inferior as presenting certain aberrations in the muscles. In

the form of the ear the gorilla is more human than any other ape, while

in the tongue the orang is the more man-like. In the stomach and liver

the gibbons approach nearest to man, then come the orang and chimpanzee,

while the gorilla has a degraded liver more resembling that of the lower

monkeys and baboons.

\_The Brains of Man and Apes.\_

We come now to that part of his organisation in which man is so much

higher than all the lower animals--the brain; and here, Mr. Mivart

informs us, the orang stands highest in rank. The height of the orang's

cerebrum in front is greater in proportion than in either the chimpanzee

or the gorilla. "On comparing the brain of man with the brains of the

orang, chimpanzee, and baboon, we find a successive decrease in the

frontal lobe, and a successive and very great increase in the relative

size of the occipital lobe. Concomitantly with this increase and

decrease, certain folds of brain substance, called 'bridging

convolutions,' which in man are conspicuously interposed between the

parietal and occipital lobes, seem as utterly to disappear in the

chimpanzee, as they do in the baboon. In the orang, however, though much

reduced, they are still to be distinguished.... The actual and absolute

mass of the brain is, however, slightly greater in the chimpanzee than

in the orang, as is the relative vertical extent of the middle part of

the cerebrum, although, as already stated, the frontal portion is higher

in the orang; while, according to M. Gratiolet, the gorilla is not only

inferior to the orang in cerebral development, but even to his smaller

African congener, the chimpanzee."[223]

On the whole, then, we find that no one of the great apes can be

positively asserted to be nearest to man in structure. Each of them

approaches him in certain characteristics, while in others it is widely

removed, giving the idea, so consonant with the theory of evolution as

developed by Darwin, that all are derived from a common ancestor, from

which the existing anthropoid apes as well as man have diverged. When,

however, we turn from the details of anatomy to peculiarities of

external form and motions, we find that, in a variety of characters, all

these apes resemble each other and differ from man, so that we may

fairly say that, while they have diverged somewhat from each other, they

have diverged much more widely from ourselves. Let us briefly enumerate

some of these differences.

\_External Differences of Man and Apes.\_

All apes have large canine teeth, while in man these are no longer than

the adjacent incisors or premolars, the whole forming a perfectly even

series. In apes the arms are proportionately much longer than in man,

while the thighs are much shorter. No ape stands really erect, a posture

which is natural in man. The thumb is proportionately larger in man, and

more perfectly opposable than in that of any ape. The foot of man

differs largely from that of all apes, in the horizontal sole, the

projecting heel, the short toes, and the powerful great toe firmly

attached parallel to the other toes; all perfectly adapted for

maintaining the erect posture, and for free motion without any aid from

the arms or hands. In apes the foot is formed almost exactly like our

hand, with a large thumb-like great toe quite free from the other toes,

and so articulated as to be opposable to them; forming with the long

finger-like toes a perfect grasping hand. The sole cannot be placed

horizontally on the ground; but when standing on a level surface the

animal rests on the outer edge of the foot with the finger and

thumb-like toes partly closed, while the hands are placed on the ground

resting on the knuckles. The illustration on the next page (Fig. 37)

shows, fairly well, the peculiarities of the hands and feet of the

chimpanzee, and their marked differences, both in form and use, from

those of man.

The four limbs, with the peculiarly formed feet and hands, are those of

arboreal animals which only occasionally and awkwardly move on level

ground. The arms are used in progression equally with the feet, and the

hands are only adapted for uses similar to those of our hands when the

animal is at rest, and then but clumsily. Lastly, the apes are all hairy

animals, like the majority of other mammals, man alone having a smooth

and almost naked skin. These numerous and striking differences, even

more than those of the skeleton and internal anatomy, point to an

enormously remote epoch when the race that was ultimately to develop

into man diverged from that other stock which continued the animal type

and ultimately produced the existing varieties of anthropoid apes.

[Illustration: FIG. 37.--Chimpanzee (Troglodytes niger).]

\_Summary of the Animal Characteristics of Man.\_

The facts now very briefly summarised amount almost to a demonstration

that man, in his bodily structure, has been derived from the lower

animals, of which he is the culminating development. In his possession

of rudimentary structures which are functional in some of the mammalia;

in the numerous variations of his muscles and other organs agreeing with

characters which are constant in some apes; in his embryonic

development, absolutely identical in character with that of mammalia in

general, and closely resembling in its details that of the higher

quadrumana; in the diseases which he has in common with other mammalia;

and in the wonderful approximation of his skeleton to those of one or

other of the anthropoid apes, we have an amount of evidence in this

direction which it seems impossible to explain away. And this evidence

will appear more forcible if we consider for a moment what the rejection

of it implies. For the only alternative supposition is, that man has

been specially created--that is to say, has been produced in some quite

different way from other animals and altogether independently of them.

But in that case the rudimentary structures, the animal-like variations,

the identical course of development, and all the other animal

characteristics he possesses are deceptive, and inevitably lead us, as

thinking beings making use of the reason which is our noblest and most

distinctive feature, into gross error.

We cannot believe, however, that a careful study of the facts of nature

leads to conclusions directly opposed to the truth; and, as we seek in

vain, in our physical structure and the course of its development, for

any indication of an origin independent of the rest of the animal world,

we are compelled to reject the idea of "special creation" for man, as

being entirely unsupported by facts as well as in the highest degree

improbable.

\_The Geological Antiquity of Man.\_

The evidence we now possess of the exact nature of the resemblance of

man to the various species of anthropoid apes, shows us that he has

little special affinity for any one rather than another species, while

he differs from them all in several important characters in which they

agree with each other. The conclusion to be drawn from these facts is,

that his points of affinity connect him with the whole group, while his

special peculiarities equally separate him from the whole group, and

that he must, therefore, have diverged from the common ancestral form

before the existing types of anthropoid apes had diverged from each

other. Now, this divergence almost certainly took place as early as the

Miocene period, because in the Upper Miocene deposits of Western Europe

remains of two species of ape have been found allied to the gibbons, one

of them, Dryopithecus, nearly as large as a man, and believed by M.

Lartet to have approached man in its dentition more than the existing

apes. We seem hardly, therefore, to have reached, in the Upper Miocene,

the epoch of the common ancestor of man and the anthropoids.

The evidence of the antiquity of man himself is also scanty, and takes

us but very little way back into the past. We have clear proof of his

existence in Europe in the latter stages of the glacial epoch, with many

indications of his presence in interglacial or even pre-glacial times;

while both the actual remains and the works of man found in the

auriferous gravels of California deep under lava-flows of Pliocene age,

show that he existed in the New World at least as early as in the

Old.[224] These earliest remains of man have been received with doubt,

and even with ridicule, as if there were some extreme improbability in

them. But, in point of fact, the wonder is that human remains have not

been found more frequently in pre-glacial deposits. Referring to the

most ancient fossil remains found in Europe--the Engis and Neanderthal

crania,--Professor Huxley makes the following weighty remark: "In

conclusion, I may say, that the fossil remains of Man hitherto

discovered do not seem to me to take us appreciably nearer to that lower

pithecoid form, by the modification of which he has, probably, become

what he is." The Californian remains and works of art, above referred

to, give no indication of a specially low form of man; and it remains an

unsolved problem why no traces of the long line of man's ancestors, back

to the remote period when he first branched off from the pithecoid type,

have yet been discovered.

It has been objected by some writers--notably by Professor Boyd

Dawkins--that man did not probably exist in Pliocene times, because

almost all the known mammalia of that epoch are distinct species from

those now living on the earth, and that the same changes of the

environment which led to the modification of other mammalian species

would also have led to a change in man. But this argument overlooks the

fact that man differs essentially from all other mammals in this

respect, that whereas any important adaptation to new conditions can be

effected in them only by a change in bodily structure, man is able to

adapt himself to much greater changes of conditions by a mental

development leading him to the use of fire, of tools, of clothing, of

improved dwellings, of nets and snares, and of agriculture. By the help

of these, without any change whatever in his bodily structure, he has

been able to spread over and occupy the whole earth; to dwell securely

in forest, plain, or mountain; to inhabit alike the burning desert or

the arctic wastes; to cope with every kind of wild beast, and to provide

himself with food in districts where, as an animal trusting to nature's

unaided productions, he would have starved.[225]

It follows, therefore, that from the time when the ancestral man first

walked erect, with hands freed from any active part in locomotion, and

when his brain-power became sufficient to cause him to use his hands in

making weapons and tools, houses and clothing, to use fire for cooking,

and to plant seeds or roots to supply himself with stores of food, the

power of natural selection would cease to act in producing modifications

of his body, but would continuously advance his mind through the

development of its organ, the brain. Hence man may have become truly

man--the species, Homo sapiens--even in the Miocene period; and while

all other mammals were becoming modified from age to age under the

influence of ever-changing physical and biological conditions, he would

be advancing mainly in intelligence, but perhaps also in stature, and by

that advance alone would be able to maintain himself as the master of

all other animals and as the most widespread occupier of the earth. It

is quite in accordance with this view that we find the most pronounced

distinction between man and the anthropoid apes in the size and

complexity of his brain. Thus, Professor Huxley tells us that "it may be

doubted whether a healthy human adult brain ever weighed less than 31

or 32 ounces, or that the heaviest gorilla brain has exceeded 20

ounces," although "a full-grown gorilla is probably pretty nearly twice

as heavy as a Bosjes man, or as many an European woman."[226] The

average human brain, however, weighs 48 or 49 ounces, and if we take the

average ape brain at only 2 ounces less than the very largest gorilla's

brain, or 18 ounces, we shall see better the enormous increase which has

taken place in the brain of man since the time when he branched off from

the apes; and this increase will be still greater if we consider that

the brains of apes, like those of all other mammals, have also increased

from earlier to later geological times.

If these various considerations are taken into account, we must conclude

that the essential features of man's structure as compared with that of

apes--his erect posture and free hands--were acquired at a comparatively

early period, and were, in fact, the characteristics which gave him his

superiority over other mammals, and started him on the line of

development which has led to his conquest of the world. But during this

long and steady development of brain and intellect, mankind must have

continuously increased in numbers and in the area which they

occupied--they must have formed what Darwin terms a "dominant race." For

had they been few in numbers and confined to a limited area, they could

hardly have successfully struggled against the numerous fierce carnivora

of that period, and against those adverse influences which led to the

extinction of so many more powerful animals. A large population spread

over an extensive area is also needed to supply an adequate number of

brain variations for man's progressive improvement. But this large

population and long-continued development in a single line of advance

renders it the more difficult to account for the complete absence of

human or pre-human remains in all those deposits which have furnished,

in such rich abundance, the remains of other land animals. It is true

that the remains of apes are also very rare, and we may well suppose

that the superior intelligence of man led him to avoid that extensive

destruction by flood or in morass which seems to have often overwhelmed

other animals. Yet, when we consider that, even in our own day, men are

not unfrequently overwhelmed by volcanic eruptions, as in Java and

Japan, or carried away in vast numbers by floods, as in Bengal and

China, it seems impossible but that ample remains of Miocene and

Pliocene man do exist buried in the most recent layers of the earth's

crust, and that more extended research or some fortunate discovery will

some day bring them to light.

\_The Probable Birthplace of Man.\_

It has usually been considered that the ancestral form of man originated

in the tropics, where vegetation is most abundant and the climate most

equable. But there are some important objections to this view. The

anthropoid apes, as well as most of the monkey tribe, are essentially

arboreal in their structure, whereas the great distinctive character of

man is his special adaptation to terrestrial locomotion. We can hardly

suppose, therefore, that he originated in a forest region, where fruits

to be obtained by climbing are the chief vegetable food. It is more

probable that he began his existence on the open plains or high plateaux

of the temperate or sub-tropical zone, where the seeds of indigenous

cereals and numerous herbivora, rodents, and game-birds, with fishes and

molluscs in the lakes, rivers, and seas supplied him with an abundance

of varied food. In such a region he would develop skill as a hunter,

trapper, or fisherman, and later as a herdsman and cultivator,--a

succession of which we find indications in the palaeolithic and

neolithic races of Europe.

In seeking to determine the particular areas in which his earliest

traces are likely to be found, we are restricted to some portion of the

Eastern hemisphere, where alone the anthropoid apes exist, or have

apparently ever existed.

There is good reason to believe, also, that Africa must be excluded,

because it is known to have been separated from the northern continent

in early tertiary times, and to have acquired its existing fauna of the

higher mammalia by a later union with that continent after the

separation from it of Madagascar, an island which has preserved for us a

sample, as it were, of the early African mammalian fauna, from which not

only the anthropoid apes, but all the higher quadrumana are

absent.[227] There remains only the great Euro-Asiatic continent; and

its enormous plateaux, extending from Persia right across Tibet and

Siberia to Manchuria, afford an area, some part or other of which

probably offered suitable conditions, in late Miocene or early Pliocene

times, for the development of ancestral man.

It is in this area that we still find that type of mankind--the

Mongolian--which retains a colour of the skin midway between the black

or brown-black of the negro, and the ruddy or olive-white of the

Caucasian types, a colour which still prevails over all Northern Asia,

over the American continents, and over much of Polynesia. From this

primary tint arose, under the influence of varied conditions, and

probably in correlation with constitutional changes adapted to peculiar

climates, the varied tints which still exist among mankind. If the

reasoning by which this conclusion is reached be sound, and all the

earlier stages of man's development from an animal form occurred in the

area now indicated, we can better understand how it is that we have as

yet met with no traces of the missing links, or even of man's existence

during late tertiary times, because no part of the world is so entirely

unexplored by the geologist as this very region. The area in question is

sufficiently extensive and varied to admit of primeval man having

attained to a considerable population, and having developed his full

human characteristics, both physical and mental, before there was any

need for him to migrate beyond its limits. One of his earliest important

migrations was probably into Africa, where, spreading westward, he

became modified in colour and hair in correlation with physiological

changes adapting him to the climate of the equatorial lowlands.

Spreading north-westward into Europe the moist and cool climate led to a

modification of an opposite character, and thus may have arisen the

three great human types which still exist. Somewhat later, probably, he

spread eastward into North-West America and soon scattered himself over

the whole continent; and all this may well have occurred in early or

middle Pliocene times. Thereafter, at very long intervals, successive

waves of migration carried him into every part of the habitable world,

and by conquest and intermixture led ultimately to that puzzling

gradation of types which the ethnologist in vain seeks to unravel.

\_The Origin of the Moral and Intellectual Nature of Man.\_

From the foregoing discussion it will be seen that I fully accept Mr.

Darwin's conclusion as to the essential identity of man's bodily

structure with that of the higher mammalia, and his descent from some

ancestral form common to man and the anthropoid apes. The evidence of

such descent appears to me to be overwhelming and conclusive. Again, as

to the cause and method of such descent and modification, we may admit,

at all events provisionally, that the laws of variation and natural

selection, acting through the struggle for existence and the continual

need of more perfect adaptation to the physical and biological

environments, may have brought about, first that perfection of bodily

structure in which he is so far above all other animals, and in

co-ordination with it the larger and more developed brain, by means of

which he has been able to utilise that structure in the more and more

complete subjection of the whole animal and vegetable kingdoms to his

service.

But this is only the beginning of Mr. Darwin's work, since he goes on to

discuss the moral nature and mental faculties of man, and derives these

too by gradual modification and development from the lower animals.

Although, perhaps, nowhere distinctly formulated, his whole argument

tends to the conclusion that man's entire nature and all his faculties,

whether moral, intellectual, or spiritual, have been derived from their

rudiments in the lower animals, in the same manner and by the action of

the same general laws as his physical structure has been derived. As

this conclusion appears to me not to be supported by adequate evidence,

and to be directly opposed to many well-ascertained facts, I propose to

devote a brief space to its discussion.

\_The Argument from Continuity.\_

Mr. Darwin's mode of argument consists in showing that the rudiments of

most, if not of all, the mental and moral faculties of man can be

detected in some animals. The manifestations of intelligence, amounting

in some cases to distinct acts of reasoning, in many animals, are

adduced as exhibiting in a much less degree the intelligence and reason

of man. Instances of curiosity, imitation, attention, wonder, and memory

are given; while examples are also adduced which may be interpreted as

proving that animals exhibit kindness to their fellows, or manifest

pride, contempt, and shame. Some are said to have the rudiments of

language, because they utter several different sounds, each of which has

a definite meaning to their fellows or to their young; others the

rudiments of arithmetic, because they seem to count and remember up to

three, four, or even five. A sense of beauty is imputed to them on

account of their own bright colours or the use of coloured objects in

their nests; while dogs, cats, and horses are said to have imagination,

because they appear to be disturbed by dreams. Even some distant

approach to the rudiments of religion is said to be found in the deep

love and complete submission of a dog to his master.[228]

Turning from animals to man, it is shown that in the lowest savages many

of these faculties are very little advanced from the condition in which

they appear in the higher animals; while others, although fairly well

exhibited, are yet greatly inferior to the point of development they

have reached in civilised races. In particular, the moral sense is said

to have been developed from the social instincts of savages, and to

depend mainly on the enduring discomfort produced by any action which

excites the general disapproval of the tribe. Thus, every act of an

individual which is believed to be contrary to the interests of the

tribe, excites its unvarying disapprobation and is held to be immoral;

while every act, on the other hand, which is, as a rule, beneficial to

the tribe, is warmly and constantly approved, and is thus considered to

be right or moral. From the mental struggle, when an act that would

benefit self is injurious to the tribe, there arises conscience; and

thus the social instincts are the foundation of the moral sense and of

the fundamental principles of morality.[229]

The question of the origin and nature of the moral sense and of

conscience is far too vast and complex to be discussed here, and a

reference to it has been introduced only to complete the sketch of Mr.

Darwin's view of the continuity and gradual development of all human

faculties from the lower animals up to savages, and from savage up to

civilised man. The point to which I wish specially to call attention is,

that to prove continuity and the progressive development of the

intellectual and moral faculties from animals to man, is not the same as

proving that these faculties have been developed by natural selection;

and this last is what Mr. Darwin has hardly attempted, although to

support his theory it was absolutely essential to prove it. Because

man's physical structure has been developed from an animal form by

natural selection, it does not necessarily follow that his mental

nature, even though developed \_pari passu\_ with it, has been developed

by the same causes only. To illustrate by a physical analogy. Upheaval

and depression of land, combined with sub-aerial denudation by wind and

frost, rain and rivers, and marine denudation on coastlines, were long

thought to account for all the modelling of the earth's surface not

directly due to volcanic action; and in the early editions of Lyell's

\_Principles of Geology\_ these are the sole causes appealed to. But when

the action of glaciers was studied and the recent occurrence of a

glacial epoch demonstrated as a fact, many phenomena--such as moraines

and other gravel deposits, boulder clay, erratic boulders, grooved and

rounded rocks, and Alpine lake basins--were seen to be due to this

altogether distinct cause. There was no breach of continuity, no sudden

catastrophe; the cold period came on and passed away in the most gradual

manner, and its effects often passed insensibly into those produced by

denudation or upheaval; yet none the less a new agency appeared at a

definite time, and new effects were produced which, though continuous

with preceding effects, were not due to the same causes. It is not,

therefore, to be assumed, without proof or against independent evidence,

that the later stages of an apparently continuous development are

necessarily due to the same causes only as the earlier stages. Applying

this argument to the case of man's intellectual and moral nature, I

propose to show that certain definite portions of it could not have been

developed by variation and natural selection alone, and that, therefore,

some other influence, law, or agency is required to account for them.

If this can be clearly shown for any one or more of the special

faculties of intellectual man, we shall be justified in assuming that

the same unknown cause or power may have had a much wider influence, and

may have profoundly influenced the whole course of his development.

\_The Origin of the Mathematical Faculty.\_

We have ample evidence that, in all the lower races of man, what may be

termed the mathematical faculty is, either absent, or, if present, quite

unexercised. The Bushmen and the Brazilian Wood-Indians are said not to

count beyond two. Many Australian tribes only have words for one and

two, which are combined to make three, four, five, or six, beyond which

they do not count. The Damaras of South Africa only count to three; and

Mr. Galton gives a curious description of how one of them was hopelessly

puzzled when he had sold two sheep for two sticks of tobacco each, and

received four sticks in payment. He could only find out that he was

correctly paid by taking two sticks and then giving one sheep, then

receiving two sticks more and giving the other sheep. Even the

comparatively intellectual Zulus can only count up to ten by using the

hands and fingers. The Ahts of North-West America count in nearly the

same manner, and most of the tribes of South America are no further

advanced.[230] The Kaffirs have great herds of cattle, and if one is

lost they miss it immediately, but this is not by counting, but by

noticing the absence of one they know; just as in a large family or a

school a boy is missed without going through the process of counting.

Somewhat higher races, as the Esquimaux, can count up to twenty by using

the hands and the feet; and other races get even further than this by

saying "one man" for twenty, "two men" for forty, and so on, equivalent

to our rural mode of reckoning by scores. From the fact that so many of

the existing savage races can only count to four or five, Sir John

Lubbock thinks it improbable that our earliest ancestors could have

counted as high as ten.[231]

When we turn to the more civilised races, we find the use of numbers

and the art of counting greatly extended. Even the Tongas of the South

Sea islands are said to have been able to count as high as 100,000. But

mere counting does not imply either the possession or the use of

anything that can be really called the mathematical faculty, the

exercise of which in any broad sense has only been possible since the

introduction of the decimal notation. The Greeks, the Romans, the

Egyptians, the Jews, and the Chinese had all such cumbrous systems, that

anything like a science of arithmetic, beyond very simple operations,

was impossible; and the Roman system, by which the year 1888 would be

written MDCCCLXXXVIII, was that in common use in Europe down to the

fourteenth or fifteenth centuries, and even much later in some places.

Algebra, which was invented by the Hindoos, from whom also came the

decimal notation, was not introduced into Europe till the thirteenth

century, although the Greeks had some acquaintance with it; and it

reached Western Europe from Italy only in the sixteenth century.[232] It

was, no doubt, owing to the absence of a sound system of numeration that

the mathematical talent of the Greeks was directed chiefly to geometry,

in which science Euclid, Archimedes, and others made such brilliant

discoveries. It is, however, during the last three centuries only that

the civilised world appears to have become conscious of the possession

of a marvellous faculty which, when supplied with the necessary tools in

the decimal notation, the elements of algebra and geometry, and the

power of rapidly communicating discoveries and ideas by the art of

printing, has developed to an extent, the full grandeur of which can be

appreciated only by those who have devoted some time (even if

unsuccessfully) to the study.

The facts now set forth as to the almost total absence of mathematical

faculty in savages and its wonderful development in quite recent times,

are exceedingly suggestive, and in regard to them we are limited to two

possible theories. Either prehistoric and savage man did not possess

this faculty at all (or only in its merest rudiments); or they did

possess it, but had neither the means nor the incitements for its

exercise. In the former case we have to ask by what means has this

faculty been so rapidly developed in all civilised races, many of which

a few centuries back were, in this respect, almost savages themselves;

while in the latter case the difficulty is still greater, for we have to

assume the existence of a faculty which had never been used either by

the supposed possessors of it or by their ancestors.

Let us take, then, the least difficult supposition--that savages

possessed only the mere rudiments of the faculty, such as their ability

to count, sometimes up to ten, but with an utter inability to perform

the very simplest processes of arithmetic or of geometry--and inquire

how this rudimentary faculty became rapidly developed into that of a

Newton, a La Place, a Gauss, or a Cayley. We will admit that there is

every possible gradation between these extremes, and that there has been

perfect continuity in the development of the faculty; but we ask, What

motive power caused its development?

It must be remembered we are here dealing solely with the capability of

the Darwinian theory to account for the origin of the \_mind\_, as well as

it accounts for the origin of the \_body\_ of man, and we must, therefore,

recall the essential features of that theory. These are, the

preservation of useful variations in the struggle for life; that no

creature can be improved beyond its necessities for the time being; that

the law acts by life and death, and by the survival of the fittest. We

have to ask, therefore, what relation the successive stages of

improvement of the mathematical faculty had to the life or death of its

possessors; to the struggles of tribe with tribe, or nation with nation;

or to the ultimate survival of one race and the extinction of another.

If it cannot possibly have had any such effects, then it cannot have

been produced by natural selection.

It is evident that in the struggles of savage man with the elements and

with wild beasts, or of tribe with tribe, this faculty can have had no

influence. It had nothing to do with the early migrations of man, or

with the conquest and extermination of weaker by more powerful peoples.

The Greeks did not successfully resist the Persian invaders by any aid

from their few mathematicians, but by military training, patriotism, and

self-sacrifice. The barbarous conquerors of the East, Timurlane and

Gengkhis Khan, did not owe their success to any superiority of intellect

or of mathematical faculty in themselves or their followers. Even if the

great conquests of the Romans were, in part, due to their systematic

military organisation, and to their skill in making roads and

encampments, which may, perhaps, be imputed to some exercise of the

mathematical faculty, that did not prevent them from being conquered in

turn by barbarians, in whom it was almost entirely absent. And if we

take the most civilised peoples of the ancient world--the Hindoos, the

Arabs, the Greeks, and the Romans, all of whom had some amount of

mathematical talent--we find that it is not these, but the descendants

of the barbarians of those days--the Celts, the Teutons, and the

Slavs--who have proved themselves the fittest to survive in the great

struggle of races, although we cannot trace their steadily growing

success during past centuries either to the possession of any

exceptional mathematical faculty or to its exercise. They have indeed

proved themselves, to-day, to be possessed of a marvellous endowment of

the mathematical faculty; but their success at home and abroad, as

colonists or as conquerors, as individuals or as nations, can in no way

be traced to this faculty, since they were almost the last who devoted

themselves to its exercise. We conclude, then, that the present gigantic

development of the mathematical faculty is wholly unexplained by the

theory of natural selection, and must be due to some altogether distinct

cause.

\_The Origin of the Musical and Artistic Faculties.\_

These distinctively human faculties follow very closely the lines of the

mathematical faculty in their progressive development, and serve to

enforce the same argument. Among the lower savages music, as we

understand it, hardly exists, though they all delight in rude musical

sounds, as of drums, tom-toms, or gongs; and they also sing in

monotonous chants. Almost exactly as they advance in general intellect,

and in the arts of social life, their appreciation of music appears to

rise in proportion; and we find among them rude stringed instruments and

whistles, till, in Java, we have regular bands of skilled performers

probably the successors of Hindoo musicians of the age before the

Mahometan conquest. The Egyptians are believed to have been the earliest

musicians, and from them the Jews and the Greeks, no doubt, derived

their knowledge of the art; but it seems to be admitted that neither the

latter nor the Romans knew anything of harmony or of the essential

features of modern music.[233] Till the fifteenth century little

progress appears to have been made in the science or the practice of

music; but since that era it has advanced with marvellous rapidity, its

progress being curiously parallel with that of mathematics, inasmuch as

great musical geniuses appeared suddenly among different nations, equal

in their possession of this special faculty to any that have since

arisen.

As with the mathematical, so with the musical faculty, it is impossible

to trace any connection between its possession and survival in the

struggle for existence. It seems to have arisen as a \_result\_ of social

and intellectual advancement, not as a \_cause\_; and there is some

evidence that it is latent in the lower races, since under European

training native military bands have been formed in many parts of the

world, which have been able to perform creditably the best modern music.

The artistic faculty has run a somewhat different course, though

analogous to that of the faculties already discussed. Most savages

exhibit some rudiments of it, either in drawing or carving human or

animal figures; but, almost without exception, these figures are rude

and such as would be executed by the ordinary inartistic child. In fact,

modern savages are, in this respect hardly equal to those prehistoric

men who represented the mammoth and the reindeer on pieces of horn or

bone. With any advance in the arts of social life, we have a

corresponding advance in artistic skill and taste, rising very high in

the art of Japan and India, but culminating in the marvellous sculpture

of the best period of Grecian history. In the Middle Ages art was

chiefly manifested in ecclesiastical architecture and the illumination

of manuscripts, but from the thirteenth to the fifteenth centuries

pictorial art revived in Italy and attained to a degree of perfection

which has never been surpassed. This revival was followed closely by the

schools of Germany, the Netherlands, Spain, France, and England, showing

that the true artistic faculty belonged to no one nation, but was fairly

distributed among the various European races.

These several developments of the artistic faculty, whether manifested

in sculpture, painting, or architecture, are evidently outgrowths of the

human intellect which have no immediate influence on the survival of

individuals or of tribes, or on the success of nations in their

struggles for supremacy or for existence. The glorious art of Greece did

not prevent the nation from falling under the sway of the less advanced

Roman; while we ourselves, among whom art was the latest to arise, have

taken the lead in the colonisation of the world, thus proving our mixed

race to be the fittest to survive.

\_Independent Proof that the Mathematical, Musical, and Artistic

Faculties have not been Developed under the Law of Natural Selection.\_

The law of Natural Selection or the survival of the fittest is, as its

name implies, a rigid law, which acts by the life or death of the

individuals submitted to its action. From its very nature it can act

only on useful or hurtful characteristics, eliminating the latter and

keeping up the former to a fairly general level of efficiency. Hence it

necessarily follows that the characters developed by its means will be

present in all the individuals of a species, and, though varying, will

not vary very widely from a common standard. The amount of variation we

found, in our third chapter, to be about one-fifth or one-sixth of the

mean value--that is, if the mean value were taken at 100, the variations

would reach from 80 to 120, or somewhat more, if very large numbers were

compared. In accordance with this law we find, that all those characters

in man which were certainly essential to him during his early stages of

development, exist in all savages with some approach to equality. In the

speed of running, in bodily strength, in skill with weapons, in

acuteness of vision, or in power of following a trail, all are fairly

proficient, and the differences of endowment do not probably exceed the

limits of variation in animals above referred to. So, in animal instinct

or intelligence, we find the same general level of development. Every

wren makes a fairly good nest like its fellows; every fox has an average

amount of the sagacity of its race; while all the higher birds and

mammals have the necessary affections and instincts needful for the

protection and bringing-up of their offspring.

But in those specially developed faculties of civilised man which we

have been considering, the case is very different. They exist only in a

small proportion of individuals, while the difference of capacity

between these favoured individuals and the average of mankind is

enormous. Taking first the mathematical faculty, probably fewer than one

in a hundred really possess it, the great bulk of the population having

no natural ability for the study, or feeling the slightest interest in

it.[234] And if we attempt to measure the amount of variation in the

faculty itself between a first-class mathematician and the ordinary run

of people who find any kind of calculation confusing and altogether

devoid of interest, it is probable that the former could not be

estimated at less than a hundred times the latter, and perhaps a

thousand times would more nearly measure the difference between them.

The artistic faculty appears to agree pretty closely with the

mathematical in its frequency. The boys and girls who, going beyond the

mere conventional designs of children, draw what they \_see\_, not what

they \_know\_ to be the shape of things; who naturally sketch in

perspective, because it is thus they see objects; who see, and represent

in their sketches, the light and shade as well as the mere outlines of

objects; and who can draw recognisable sketches of every one they know,

are certainly very few compared with those who are totally incapable of

anything of the kind. From some inquiries I have made in schools, and

from my own observation, I believe that those who are endowed with this

natural artistic talent do not exceed, even if they come up to, one per

cent of the whole population.

The variations in the amount of artistic faculty are certainly very

great, even if we do not take the extremes. The gradations of power

between the ordinary man or woman "who does not draw," and whose

attempts at representing any object, animate or inanimate, would be

laughable, and the average good artist who, with a few bold strokes, can

produce a recognisable and even effective sketch of a landscape, a

street, or an animal, are very numerous; and we can hardly measure the

difference between them at less than fifty or a hundred fold.

The musical faculty is undoubtedly, in its lower forms, less uncommon

than either of the preceding, but it still differs essentially from the

necessary or useful faculties in that it is almost entirely wanting in

one-half even of civilised men. For every person who draws, as it were

instinctively, there are probably five or ten who sing or play without

having been taught and from mere innate love and perception of melody

and harmony.[235] On the other hand, there are probably about as many

who seem absolutely deficient in musical perception, who take little

pleasure in it, who cannot perceive discords or remember tunes, and who

could not learn to sing or play with any amount of study. The

gradations, too, are here quite as great as in mathematics or pictorial

art, and the special faculty of the great musical composer must be

reckoned many hundreds or perhaps thousands of times greater than that

of the ordinary "unmusical" person above referred to.

It appears then, that, both on account of the limited number of persons

gifted with the mathematical, the artistic, or the musical faculty, as

well as from the enormous variations in its development, these mental

powers differ widely from those which are essential to man, and are, for

the most part, common to him and the lower animals; and that they could

not, therefore, possibly have been developed in him by means of the law

of natural selection.

\* \* \* \* \*

We have thus shown, by two distinct lines of argument, that faculties

are developed in civilised man which, both in their mode of origin,

their function, and their variations, are altogether distinct from those

other characters and faculties which are essential to him, and which

have been brought to their actual state of efficiency by the necessities

of his existence. And besides the three which have been specially

referred to, there are others which evidently belong to the same class.

Such is the metaphysical faculty, which enables us to form abstract

conceptions of a kind the most remote from all practical applications,

to discuss the ultimate causes of things, the nature and qualities of

matter, motion, and force, of space and time, of cause and effect, of

will and conscience. Speculations on these abstract and difficult

questions are impossible to savages, who seem to have no mental faculty

enabling them to grasp the essential ideas or conceptions; yet whenever

any race attains to civilisation, and comprises a body of people who,

whether as priests or philosophers, are relieved from the necessity of

labour or of taking an active part in war or government, the

metaphysical faculty appears to spring suddenly into existence,

although, like the other faculties we have referred to, it is always

confined to a very limited proportion of the population.

In the same class we may place the peculiar faculty of wit and humour,

an altogether natural gift whose development appears to be parallel with

that of the other exceptional faculties. Like them, it is almost unknown

among savages, but appears more or less frequently as civilisation

advances and the interests of life become more numerous and more

complex. Like them, too, it is altogether removed from utility in the

struggle for life, and appears sporadically in a very small percentage

of the population; the majority being, as is well known, totally unable

to say a witty thing or make a pun even to save their lives.[236]

\_The Interpretation of the Facts.\_

The facts now set forth prove the existence of a number of mental

faculties which either do not exist at all or exist in a very

rudimentary condition in savages, but appear almost suddenly and in

perfect development in the higher civilised races. These same faculties

are further distinguished by their sporadic character, being well

developed only in a very small proportion of the community; and by the

enormous amount of variation in their development, the higher

manifestations of them being many times--perhaps a hundred or a thousand

times--stronger than the lower. Each of these characteristics is totally

inconsistent with any action of the law of natural selection in the

production of the faculties referred to; and the facts, taken in their

entirety, compel us to recognise some origin for them wholly distinct

from that which has served to account for the animal

characteristics--whether bodily or mental--of man.

The special faculties we have been discussing clearly point to the

existence in man of something which he has not derived from his animal

progenitors--something which we may best refer to as being of a

spiritual essence or nature, capable of progressive development under

favourable conditions. On the hypothesis of this spiritual nature,

superadded to the animal nature of man, we are able to understand much

that is otherwise mysterious or unintelligible in regard to him,

especially the enormous influence of ideas, principles, and beliefs over

his whole life and actions. Thus alone we can understand the constancy

of the martyr, the unselfishness of the philanthropist, the devotion of

the patriot, the enthusiasm of the artist, and the resolute and

persevering search of the scientific worker after nature's secrets. Thus

we may perceive that the love of truth, the delight in beauty, the

passion for justice, and the thrill of exultation with which we hear of

any act of courageous self-sacrifice, are the workings within us of a

higher nature which has not been developed by means of the struggle for

material existence.

It will, no doubt, be urged that the admitted continuity of man's

progress from the brute does not admit of the introduction of new

causes, and that we have no evidence of the sudden change of nature

which such introduction would bring about. The fallacy as to new causes

involving any breach of continuity, or any sudden or abrupt change, in

the effects, has already been shown; but we will further point out that

there are at least three stages in the development of the organic world

when some new cause or power must necessarily have come into action.

The first stage is the change from inorganic to organic, when the

earliest vegetable cell, or the living protoplasm out of which it arose,

first appeared. This is often imputed to a mere increase of complexity

of chemical compounds; but increase of complexity, with consequent

instability, even if we admit that it may have produced protoplasm as a

chemical compound, could certainly not have produced \_living\_

protoplasm--protoplasm which has the power of growth and of

reproduction, and of that continuous process of development which has

resulted in the marvellous variety and complex organisation of the whole

vegetable kingdom. There is in all this something quite beyond and

apart from chemical changes, however complex; and it has been well said

that the first vegetable cell was a new thing in the world, possessing

altogether new powers--that of extracting and fixing carbon from the

carbon-dioxide of the atmosphere, that of indefinite reproduction, and,

still more marvellous, the power of variation and of reproducing those

variations till endless complications of structure and varieties of form

have been the result. Here, then, we have indications of a new power at

work, which we may term \_vitality\_, since it gives to certain forms of

matter all those characters and properties which constitute Life.

The next stage is still more marvellous, still more completely beyond

all possibility of explanation by matter, its laws and forces. It is the

introduction of sensation or consciousness, constituting the fundamental

distinction between the animal and vegetable kingdoms. Here all idea of

mere complication of structure producing the result is out of the

question. We feel it to be altogether preposterous to assume that at a

certain stage of complexity of atomic constitution, and as a necessary

result of that complexity alone, an \_ego\_ should start into existence, a

thing that \_feels\_, that is \_conscious\_ of its own existence. Here we

have the certainty that something new has arisen, a being whose nascent

consciousness has gone on increasing in power and definiteness till it

has culminated in the higher animals. No verbal explanation or attempt

at explanation--such as the statement that life is the result of the

molecular forces of the protoplasm, or that the whole existing organic

universe from the amaeba up to man was latent in the fire-mist from

which the solar system was developed--can afford any mental

satisfaction, or help us in any way to a solution of the mystery.

The third stage is, as we have seen, the existence in man of a number of

his most characteristic and noblest faculties, those which raise him

furthest above the brutes and open up possibilities of almost indefinite

advancement. These faculties could not possibly have been developed by

means of the same laws which have determined the progressive development

of the organic world in general, and also of man's physical

organism.[237]

These three distinct stages of progress from the inorganic world of

matter and motion up to man, point clearly to an unseen universe--to a

world of spirit, to which the world of matter is altogether subordinate.

To this spiritual world we may refer the marvellously complex forces

which we know as gravitation, cohesion, chemical force, radiant force,

and electricity, without which the material universe could not exist for

a moment in its present form, and perhaps not at all, since without

these forces, and perhaps others which may be termed atomic, it is

doubtful whether matter itself could have any existence. And still more

surely can we refer to it those progressive manifestations of Life in

the vegetable, the animal, and man--which we may classify as

unconscious, conscious, and intellectual life,--and which probably

depend upon different degrees of spiritual influx. I have already shown

that this involves no necessary infraction of the law of continuity in

physical or mental evolution; whence it follows that any difficulty we

may find in discriminating the inorganic from the organic, the lower

vegetable from the lower animal organisms, or the higher animals from

the lowest types of man, has no bearing at all upon the question. This

is to be decided by showing that a change in essential nature (due,

probably, to causes of a higher order than those of the material

universe) took place at the several stages of progress which I have

indicated; a change which may be none the less real because absolutely

imperceptible at its point of origin, as is the change that takes place

in the curve in which a body is moving when the application of some new

force causes the curve to be slightly altered.

\_Concluding Remarks.\_

Those who admit my interpretation of the evidence now adduced--strictly

scientific evidence in its appeal to facts which are clearly what ought

\_not\_ to be on the materialistic theory--will be able to accept the

spiritual nature of man, as not in any way inconsistent with the theory

of evolution, but as dependent on those fundamental laws and causes

which furnish the very materials for evolution to work with. They will

also be relieved from the crushing mental burthen imposed upon those

who--maintaining that we, in common with the rest of nature, are but

products of the blind eternal forces of the universe, and believing also

that the time must come when the sun will lose his heat and all life on

the earth necessarily cease--have to contemplate a not very distant

future in which all this glorious earth--which for untold millions of

years has been slowly developing forms of life and beauty to culminate

at last in man--shall be as if it had never existed; who are compelled

to suppose that all the slow growths of our race struggling towards a

higher life, all the agony of martyrs, all the groans of victims, all

the evil and misery and undeserved suffering of the ages, all the

struggles for freedom, all the efforts towards justice, all the

aspirations for virtue and the wellbeing of humanity, shall absolutely

vanish, and, "like the baseless fabric of a vision, leave not a wrack

behind."

As contrasted with this hopeless and soul-deadening belief, we, who

accept the existence of a spiritual world, can look upon the universe as

a grand consistent whole adapted in all its parts to the development of

spiritual beings capable of indefinite life and perfectibility. To us,

the whole purpose, the only \_raison d'Ãªtre\_ of the world--with all its

complexities of physical structure, with its grand geological progress,

the slow evolution of the vegetable and animal kingdoms, and the

ultimate appearance of man--was the development of the human spirit in

association with the human body. From the fact that the spirit of

man--the man himself--\_is\_ so developed, we may well believe that this

is the only, or at least the best, way for its development; and we may

even see in what is usually termed "evil" on the earth, one of the most

efficient means of its growth. For we know that the noblest faculties of

man are strengthened and perfected by struggle and effort; it is by

unceasing warfare against physical evils and in the midst of difficulty

and danger that energy, courage, self-reliance, and industry have become

the common qualities of the northern races; it is by the battle with

moral evil in all its hydra-headed forms, that the still nobler

qualities of justice and mercy and humanity and self-sacrifice have been

steadily increasing in the world. Beings thus trained and strengthened

by their surroundings, and possessing latent faculties capable of such

noble development, are surely destined for a higher and more permanent

existence; and we may confidently believe with our greatest living

poet--

That life is not as idle ore,

But iron dug from central gloom,

And heated hot with burning fears,

And dipt in baths of hissing tears,

And batter'd with the shocks of doom

To shape and use.

We thus find that the Darwinian theory, even when carried out to its

extreme logical conclusion, not only does not oppose, but lends a

decided support to, a belief in the spiritual nature of man. It shows us

how man's body may have been developed from that of a lower animal form

under the law of natural selection; but it also teaches us that we

possess intellectual and moral faculties which could not have been so

developed, but must have had another origin; and for this origin we can

only find an adequate cause in the unseen universe of Spirit.

FOOTNOTES:

[Footnote 218: \_Descent of Man\_, pp. 41-43; also pp. 13-15.]

[Footnote 219: \_Man's Place in Nature\_, p. 64.]

[Footnote 220: \_Man's Place in Nature\_, p. 67. See Figs. of Embryos of

Man and Dog in Darwin's \_Descent of Man\_, p. 10.]

[Footnote 221: \_The Descent of Man\_, pp. 7, 8.]

[Footnote 222: \_Man and Apes.\_ By St. George Mivart, F.R.S., 1873. It is

an interesting fact (for which I am indebted to Mr. E.B. Poulton) that

the human embryo possesses the extra rib and wrist-bone referred to

above in (2) and (4) as occurring in some of the apes.]

[Footnote 223: \_Man and Apes\_, pp. 138, 144.]

[Footnote 224: For a sketch of the evidence of Man's Antiquity in

America, see \_The Nineteenth Century\_ for November 1887.]

[Footnote 225: This subject was first discussed in an article in the

\_Anthropological Review\_, May 1864, and republished in my \_Contributions

to Natural Selection\_, chap, ix, in 1870.]

[Footnote 226: \_Man's Place in Nature\_, p. 102.]

[Footnote 227: For a full discussion of this question, see the author's

\_Geographical Distribution of Animals\_, vol. i. p. 285.]

[Footnote 228: For a full discussion of all these points, see \_Descent

of Man\_, chap. iii.]

[Footnote 229: \_Descent of Man\_, chap. iv.]

[Footnote 230: Lubbock's \_Origin of Civilisation\_, fourth edition, pp.

434-440; Tylor's \_Primitive Culture\_, chap. vii.]

[Footnote 231: It has been recently stated that some of these facts are

erroneous, and that some Australians can keep accurate reckoning up to

100, or more, when required. But this does not alter the general fact

that many low races, including the Australians, have no words for high

numbers and never require to use them. If they are now, with a little

practice, able to count much higher, this indicates the possession of a

faculty which could not have been developed under the law of utility

only, since the absence of words for such high numbers shows that they

were neither used nor required.]

[Footnote 232: Article Arithmetic in \_Eng. Cyc. of Arts and Sciences\_.]

[Footnote 233: See "History of Music," in \_Eng. Cyc.\_, Science and Arts

Division.]

[Footnote 234: This is the estimate furnished me by two mathematical

masters in one of our great public schools of the proportion of boys who

have any special taste or capacity for mathematical studies. Many more,

of course, can be drilled into a fair knowledge of elementary

mathematics, but only this small proportion possess the natural faculty

which renders it possible for them ever to rank high as mathematicians,

to take any pleasure in it, or to do any original mathematical work.]

[Footnote 235: I am informed, however, by a music master in a large

school that only about one per cent have real or decided musical talent,

corresponding curiously with the estimate of the mathematicians.]

[Footnote 236: In the latter part of his essay on Heredity (pp. 91-93 of

the volume of \_Essays\_), Dr. Weismann refers to this question of the

origin of "talents" in man, and, like myself, comes to the conclusion

that they could not be developed under the law of natural selection. He

says: "It may be objected that, in man, in addition to the instincts

inherent in every individual, special individual predispositions are

also found, of such a nature that it is impossible they can have arisen

by individual variations of the germ-plasm. On the other hand, these

predispositions--which we call talents--cannot have arisen through

natural selection, because life is in no way dependent on their

presence, and there seems to be no way of explaining their origin except

by an assumption of the summation of the skill attained by exercise in

the course of each single life. In this case, therefore, we seem at

first sight to be compelled to accept the transmission of acquired

characters." Weismann then goes on to show that the facts do not support

this view; that the mathematical, musical, or artistic faculties often

appear suddenly in a family whose other members and ancestors were in no

way distinguished; and that even when hereditary in families, the talent

often appears at its maximum at the commencement or in the middle of the

series, not increasing to the end, as it should do if it depended in any

way on the transmission of acquired skill. Gauss was not the son of a

mathematician, nor Handel of a musician, nor Titian of a painter, and

there is no proof of any special talent in the ancestors of these men of

genius, who at once developed the most marvellous pre-eminence in their

respective talents. And after showing that such great men only appear at

certain stages of human development, and that two or more of the special

talents are not unfrequently combined in one individual, he concludes

thus--

"Upon this subject I only wish to add that, in my opinion,

talents do not appear to depend upon the improvement of any

special mental quality by continued practice, but they are the

expression, and to a certain extent the bye-product, of the

human mind, which is so highly developed in all directions."

It will, I think, be admitted that this view hardly accounts for the

existence of the highly peculiar human faculties in question.]

[Footnote 237: For an earlier discussion of this subject, with some

wider applications, see the author's \_Contributions to the Theory of

Natural Selection\_, chap. x.]

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