INTRODUCTION.

All flesh is not the same flesh: but there is one kind of flesh of men, another flesh of beasts, another of fishes, and another of birds.

SECTION I.

THE STUDY OF VARIATION.

To solve the problem of the forms of living things is the aim with which the naturalist of to-day comes to his work. How have living things become what they are, and what are the laws which govern their forms? These are the questions which the naturalist has set himself to answer.

It is more than thirty years since the *Origin of Species* was written, but for many these questions are in no sense answered yet. In owning that it is so, we shall not honour Darwin's memory the less; for whatever may be the part which shall be finally assigned to Natural Selection, it will always be remembered that it was through Darwin's work that men saw for the first time that the problem is one which man may reasonably hope to solve. If Darwin did not solve the problem himself, he first gave us the hope of a solution, perhaps a greater thing. How great a feat this was, we who have heard it all from childhood can scarcely know.

In the present work an attempt is made to find a way of attacking parts of the problem afresh, and it will be profitable first to state formally the conditions of the problem and to examine the methods by which the solution has been attempted before. This consideration shall be as brief as it can be made.

The forms of living things have many characters: to solve the problem completely account must be taken of all. Perhaps no character of form is common to all living things; on the contrary their forms are almost infinitely diverse. Now in those attempts to solve the problem which have been the best, it is this diversity of form which is taken as the chief attribute, and the attempt to solve the general problem is begun by trying to trace the modes by which the diversity has been produced. In the shape in which it has been most studied, the problem is thus the problem of Species. Obscurity has been brought into the treatment of the question through want of recognition of the fact that this is really only a part of the general problem, which would still remain if there were only one species. Nevertheless the problem of Species is so tangible a part of the whole that it is perhaps the best point of departure. For our present purpose we cannot begin better than by stating it concisely.

The forms of living things are diverse. They may nevertheless be separated into Specific Groups or Species, the members of each such group being nearly alike, while they are less like the members of any other Specific Group. [The Specific Groups may by their degrees of resemblance be arranged in Generic Groups and so on.]

The individuals of each Specific Group, though alike, are not identical in form, but exhibit differences, and in these differences they may even more or less nearly approach the form characteristic of another Specific Group. It is true, besides, that in the case of many Specific Groups which have been separated from each other, intermediate forms are found which form a continuous series of gradations, passing insensibly from the form characteristic of one Species to that characteristic of another. In such cases the distinction between the two groups for purposes of classification is not retained.

The fact that in certain cases there are forms transitional between groups which are sufficiently different to have been thought to be distinct, is a very important fact which must not be lost sight of; but though now a good many such cases are known, it remains none the less true that at a given point of time, the forms of living things may be arranged in Specific Groups, and that between the immense majority of these there are no transitional forms. There are therefore between these Specific Groups differences which are Specific.

No definition of a Specific Difference has been found, perhaps because these Differences are indefinite and hence not capable of definition. But the forms of living things, taken at a given moment, do nevertheless most certainly form a discontinuous series and not a continuous series. This is true of the world as we see it now, and there is no good reason for thinking that it has ever been otherwise. So much is being said of the mutability of species that this, which is the central fact of Natural History, is almost lost sight of, but if ever the problem is to be solved this fact must be boldly faced. There is nothing to be gained by shirking or trying to forget it.

The existence, then, of Specific Differences is one of the characteristics of the forms of living things. This is no merely subjective conception, but an objective, tangible fact. This is the first part of the problem.

In the next place, not only do Specific forms exist in Nature, but they exist in such a way as to fit the place in Nature in which they are placed; that is to say, the Specific form which an organism has, is *adapted* to the position which it fills. This again is a relative truth, for the adaptation is not absolute.

These two facts constitute the problem:

I. *The forms of living things are various and, on the whole, are Discontinuous or Specific.*

II. *The Specific forms, on the whole, fit the places they have to live in.*

How have these Discontinuous forms been brought into existence, and how is it they are thus adapted? This is the question the naturalist is to answer. To answer it completely he must find (1) *The modes* and (2) *The causes* by which these things have come to pass.

Before considering the ways in which naturalists have tried to answer these questions, it is necessary to look at some other phenomena characteristic of Life. We have said that *at a given moment*, or point of time, the specific forms of living things compose a discontinuous series. The element of time thus introduced is of consequence, and leads to important considerations. For the condition of the organized world is not a fixed condition, but changes from moment to moment, and that which can be predicated of its condition at one moment may not at any other point of time be true. This process of change is brought about partly by progressive changes in the bodies of the individuals themselves, but chiefly by the constant succession of individuals, the parents dying, their offspring succeeding them. It is then a matter of observation that the offspring born of parents belonging to any one Specific Group do as a rule conform to that Specific Group themselves, and that the form of the body, the mechanisms and the instincts of the offspring, are on the whole similar to those which their parents had. But like most general assertions about living things this is true not absolutely but relatively only. For though on the whole the offspring is like the parent or parents, its form is perhaps never identical with theirs, but generally differs from it perceptibly and sometimes materially. To this phenomenon, namely, the occurrence of differences between the structure, the instincts, or other elements which compose the mechanism of the offspring, and those which were proper to the parent, the name **Variation** has been given.

We have seen above that the two leading facts respecting the forms of living things are first that they shew specific differentiation, and secondly that they are adapted. To these we may now add a third, that in the succession from parent to offspring there is, or may be, Variation. It is upon the fact of the existence of this phenomenon of Variation that all inductive theories of Evolution have been based.

The suggestion which thus forms the common ground of these theories is this:—May not the Specific Differences between Species and Species have come about through and be compounded of the individual differences between parent and offspring? May not Specific Differentiation have resulted from Individual Variation? This suggestion has been spoken of as the Doctrine of Common Descent, for it asserts that there is between living things a community of descent.

In what follows it will be assumed that this Doctrine of Descent is true. It should be admitted from the first that the truth of the doctrine has never been proved. There is nevertheless a great balance of evidence in its favour, but it finds its support not so much in direct observation as in the difficulty of forming any alternative hypothesis. The Theory of Descent involves and asserts that all living things are genetically connected, and this principle is at least not contrary to observation; while any alternative hypothesis involves the idea of Separate Creation which by common consent is now recognized as absurd. In favour of the Doctrine of Common Descent there is a balance of evidence; it is besides accepted by most naturalists; lastly if it is not true we can get no further with the problem: but inasmuch as it is unproven, it is right that we should explicitly recognize that it is in part an assumption, and that we have adopted it as a postulate.

The Doctrine of Descent being assumed, two chief solutions of the problem have been offered, both starting alike from this common ground. Let us now briefly consider each of them.

A. *Lamarck's Solution.* So many ambiguities and pitfalls are in the way of any who may try to re-state, in a few words, the theory propounded in the *Philosophie Zoologique,* that it is with great diffidence that the following account of it is given.

Lamarck points out that living things can in some measure adapt themselves both structurally and physiologically to new circumstances, and that in certain cases the adaptability is present in a high degree. He suggests that by inheritance and perfection of such adaptations they may have become what they are, and that thus specific forms and mechanisms have been produced, as it were, by sheer force of circumstances. On this view it is assumed that to the demands made on it by the environment the organism makes an appropriate structural and physiological response; in other words, that there is in living things a certain *tension,* by which they respond to environmental pressure and fit the place they are in, somewhat as a fluid fits a vessel.

This is not, I think, a misrepresentation of Lamarck's theory. It amounts, in other words, to a proposal to regard organisms as machines which have the power of Adaptation as one of their fundamental and inherent qualities or attributes.

Without discussing this solution, we may note that it aims at being a *complete* solution of both

(1) The *existence* and *persistence* of differing forms,
(2) The fact that the differing forms are *adapted* to different conditions;
and (3) The *causes of the Variation* by which the diversity has occurred.

B. *Darwin's Solution.* Darwin, without suggesting causes of Variation, points out that since (1) Variations occur—which they are known to do—and since (2) some of the variations are in the direction of adaptation and others are not—which is a necessity—it will result from the conditions of the Struggle for Existence that those better adapted will *on the whole* persist and the less adapted will on the whole be lost. In the result, therefore, there will be a diversity of forms, *more or less* adapted to the states in which they are placed, and this is very much the observed condition of living things.

We may note that this solution does not aim at being a complete solution like Lamarck's, for as to the *causes* of Variation it makes no suggestion.

The arguments by which these several solutions are supported, and the difficulties which are in the way of each, are so familiar that it would be unprofitable to detail them. On our present knowledge the matter is talked out. Those who are satisfied with either solution are likely to remain so.

It may be remarked however that the observed cases of adaptation occurring in the way demanded on Lamarck's theory are very few, and as time goes on this deficiency of facts begins to be significant. Natural Selection on the other hand is obviously a 'true cause,' at the least.

In the way of both solutions there is one cardinal difficulty which in its most general form may be thus expressed. According to both theories, specific diversity of form is consequent upon diversity of environment, and diversity of environment is thus the ultimate measure of diversity of specific form. Here then we meet the difficulty that diverse environments often shade into each other insensibly and form a continuous series, whereas the Specific Forms of life which are subject to them on the whole form a Discontinuous Series. The immense significance of this difficulty will be made more apparent in the course of this work. The difficulty is here put generally. Particular instances have been repeatedly set forth. Temperature, altitude, depth of water, salinity, in fact most of the elements which make up the physical environment are continuous in their gradations, while, as a rule, the forms of life are discontinuous[1]. Besides this, forms which

[1] It may be objected that to any organism the other organisms coexisting with it are as serious a factor of the environment as the strictly physical components; and that inasmuch as these coexisting organisms are discontinuous species, the

are apparently identical live under conditions which are apparently very different, while species which though closely allied are constantly distinct are found under conditions which are apparently the same. If we would make these facts accord with the view that it is diversity of environment which is the measure of diversity of specific form, it is necessary to suppose either (1) that our estimate of similarity of forms, or of environment, is wholly untrustworthy, or else (2) that there is a wide area of environmental or structural divergence within which no sensible result is produced: that is to say, that the relation between environment and structure is not finely adjusted. But either of these admissions is serious; for if we grant the former we abrogate the right of judgment, and are granting that our proposed solutions are mere hypotheses which we have no power to test, while if we admit the latter, we admit that environment cannot so far be either the directing cause or the limiting cause of Specific Differences, though the first is essential to Lamarck's Theory, and the second is demanded by the doctrine of Natural Selection.

Such then, put very briefly, are the two great theories, and this is one of the chief difficulties which beset them. We must now pass to our proper work.

We have to consider whether it is not possible to get beyond the present position and to penetrate further into this mystery of Specific Forms. The main obstacle being our own ignorance, the first question to be settled is what kind of knowledge would be of the most value, and which of the many unknowns may be determined with the greatest profit. To decide this we must return once more to the ground which is common to all the inductive theories of Evolution alike. Now all these different theories start from the hypothesis that the different forms of life are related to each other, and that their diversity is due to Variation. On this hypothesis, therefore, Variation, whatever may be its cause, and however it may be limited, is the essential phenomenon of Evolution. Variation, in fact, *is* Evolution. The readiest way, then, of solving the problem of Evolution is to study the facts of Variation.

SECTION II.

Alternative Methods.

The Study of Variation is therefore suggested as the method which is on the whole more likely than any other to give us the kind of knowledge we are wanting. It should be tried not so much in the hope that it will give any great insight into those

element of discontinuity may thus be introduced. This is true, but it does not help in the attempt to find the cause of the original discontinuity of the coexisting organisms.

relations of cause and effect of which Evolution is the expression, but merely as an empirical means of getting at the outward and visible phenomena which constitute Evolution. On the hypothesis of Common Descent, the forms of living things are succeeding each other, passing across the stage of the earth in a constant procession. To find the laws of the succession it will be best for us to stand as it were aside and to watch the procession as it passes by. No amount of knowledge of individual forms will tell us the laws or even the manner of the succession, nor shall we be much helped by comparison of forms of whose descent we know nothing save by speculation. To study Variation it must be seen at the moment of its beginning. For comparison we require the parent and the varying offspring together. To find out the nature of the progression we require, simultaneously, at least two consecutive terms of the progression. Evidence of this kind can be obtained in no other way than by the study of actual and contemporary cases of Variation. To the solution of this question collateral methods of research will not contribute much.

Since Darwin wrote, several of these collateral methods have been tried, and though a great deal has thus been done and a vast number of facts have been established, yet the advance towards a knowledge of the steps by which Evolution proceeds has been almost nothing. It will not perhaps be wandering unduly if we consider very shortly the reason of this, for the need for the Study of Variation will thereby be made more plain.

Before the publication of the *Origin of Species* the work of naturalists was chiefly devoted to the indiscriminate accumulation of facts. By most the work was done for its own sake in the strictest sense. In the minds of some there was of course a hope that the gathering of knowledge would at last lead on to something more, but this hope was for the most part formless and vague. With the promulgation of the Doctrine of Descent the whole course of the study was changed. The enthusiasm of naturalists ran altogether into new channels; a new class of facts was sought and the value of Zoological discovery was judged by a new criterion. The change was thus a change of aim, and consequently a change of method. From a large field of possibilities the choice fell chiefly upon two methods, each having a definite relation to the main problem. The first of these is the Embryological Method, and the second may be spoken of as the Study of Adaptation. The pursuit of these two methods was the direct outcome of Darwin's work, and such great hopes have been set on them that before starting on a new line we shall do well to examine carefully their proper scope and see whither each of them may reasonably be expected to lead.

It is besides in the examination of these methods and in observing the exact point at which they have failed, that the need for the Study of Variation will become most evident.

When the Theory of Evolution first gained a hearing it became of the highest importance that it should be put to some test which should shew whether it was true or not. In comparison with this all other questions sank into insignificance.

Now, the principle which has been called the Law of von Baer, provided the means for such a test. By this principle it is affirmed that the history of the individual represents the history of the Species. If then it should be found that organisms in their development pass through stages in which they resemble other forms, this would be *prima facie* a reason for believing them to be genetically connected. The general truth of the Theory of Descent might thus be tested by the facts of development. For this reason the Study of Embryology superseded all others. It is now, of course, generally admitted that the Theory has stood this test, and that the facts of Embryology do support the Doctrine of Community of Descent.

But the claims of Embryology did not stop here. In addition to the application of the method to the general Theory of Descent, it has been sought to apply the facts of Embryology to solve particular questions of the descent of particular forms. It has been maintained that if it is true that the history of the individual repeats the history of the Species, we may in the study of Development see not only that the various forms are related, but also the exact lines of Descent of particular forms. In this way Embryology was to provide us with the history of Evolution.

The survey of the development of animals from this point of view is now complete for most forms of life, and in all essential points; we are now therefore in a position to estimate its value. It will, I think, before long be admitted that in this attempt to extend the general proposition to particular questions of Descent the embryological method has failed. The reason for this is obvious. The principle of von Baer was never more than a rough approximation to the truth and was never suited to the solution of particular problems. It is curious to notice upon how very slight a basis of evidence this widely received principle really rests. It has been established almost entirely by inference and it has been demonstrated by actual observation in scarcely a single instance.

For the stages through which a *particular* organism passes in the course of its development are admissible as evidence of its pedigree only when it shall have been proved as a *general* truth that the development of individuals does follow the lines on which the species developed. The proof, however, of this general proposition does not rest on direct observation but on the indirect evidence that particular organisms at certain stages in their development resemble other organisms, and hence it is assumed that they are descended from those forms. Thus the truth of the general proposition is established by assuming it true in special cases, while its applicability to special cases rests on its having been accepted as a general truth.

Probably however the apologists of this method would maintain that the principle of von Baer, though its truth has not been demonstrated directly, yet belongs to the class of "True Hypotheses." To establish the truth of a hypothesis in a case like the present in which the number of possible hypotheses is not limited, it should at least be shewn that its application in *all* known instances is so precise, so simple, and in such striking accordance with ascertained facts, that its truth is felt to be irresistible.

Nothing like this can be said of the principle of von Baer. Even if it be generally true that the development of a form is a record of its descent, it has never been suggested that the record is complete.

Allowance must constantly be made for the omission of stages, for the intercalation of stages, for degeneration, for the presence of organs specially connected with larval or embryonic life, for the interference of yolk and so forth. But what this allowance should be and in what cases it should be made has never been determined.

More than this: closely allied forms often develop on totally different plans; for example, *Balanoglossus Kowalevskii* has an opaque larva which creeps in the sand, while the other species of the family have a transparent larva which swims at the surface of the sea; the germinal layers of the Guinea-pig when compared with those of the Rabbit are completely inverted, and so on. These are not isolated cases, for examples of the same kind occur in almost every group and in the development of nearly all the systems of organs. When these things are so, who shall determine which developmental process is ancestral and which is due to secondary change? By what rules may secondary changes be recognized as such? Do transparent larvæ swimming at the surface of the sea reproduce the ancestral type or does the opaque larva creeping in the mud shew us the primitive form? Each investigator has answered these questions in the manner which seemed best to himself.

There is no rule to guide us in these things and there is no canon by which we may judge the worth of the evidence. It is perhaps not too much to say that the main features of the development of nearly every type of animal are now ascertained, and on this knowledge elaborate and various tables of phylogeny have been constructed, each differing from the rest and all plausible; but it would be difficult to name a single case in which the immediate pedigree of a species is actually known.

The Embryological Method then has failed not for want of knowledge of the visible facts of development but through ignorance of the principles of Evolution. The principle of von Baer, taken by itself, is clearly incapable of interpreting the phenomena of development. We are endeavouring by means of a mass of conflicting evidence to reconstruct the series of Descent, but of the laws which govern such a series we are ignorant. In the interpretation of Embryological evidence it is constantly necessary to make certain hypotheses as to the course of Variation in the past, but before this can be done it is surely necessary that we should have some knowledge of the modes of Variation in the present. When we shall know something of the nature of the variations which are now occurring in animals and the steps by which they are now progressing before our eyes, we shall be in a position to surmise what their past has been; for we shall then know what changes are possible to them and what are not. In the absence of such knowledge, any person is at liberty to postulate the occurrence of variations on any lines which may suggest themselves to him, a liberty which has of late been freely used. Embryology has provided us with a magnificent body of facts, but the interpretation of the facts is still to seek.

The other method which, since Darwin's work, has attracted most attention is the study of the mechanisms by which organisms are adapted to the conditions in which they live. This study of Adaptation and of the utility of structures exercises an extraordinary fascination over the minds of some and it is most important that its proper use and scope should be understood.

We have seen that the Embryological Method owed its importance to its value as a mode of testing the truth of the Theory of Evolution: in the same way the Study of Adaptation was undertaken as a test of the Theory of Natural Selection.

Amongst many classes of animals, complex structures are present which do not seem to contribute directly to the well-being of their possessors. By many it has been felt that the persistent occurrence of organs of this class is a difficulty, on the hypothesis that there is a tendency for useful structures to be retained and for useless parts to be lost. In consequence it has been anticipated that sufficient research would reveal the manner in which these parts are directly useful. The amount of evidence collected with this object is now enormous, and most astonishing ingenuity has been evoked in the interpretation of it. A discussion of the truth of the conclusions thus put forward is of course apart from our present purpose, which is to examine the logical value of this method of research as a means of attacking the problem of Evolution. With regard to the results it has attained it must suffice to notice the fact that while the functions of many problematical organs have been conjectured, in some cases perhaps rightly, there remain whole groups of common phenomena of this kind, which are still almost untouched even by speculation, and structures and instincts are found in the best known forms, as to the "utility" of which no one has made even a plausible surmise. All this is familiar to every one and every one knows the various answers that have been made.

It is not quite fair to judge such a method by the imperfection of its results, but in one respect the deficiency of results obtained by the Study of Adaptation is very striking, and though this has often been recognized it must be again and again insisted on as a thing to be kept always in view. The importance of this consideration will be seen when the evidence of Variation is examined. The Study of Adaptation ceases to help us at the exact point at which help is most needed. We are seeking for the cause of the differences between species and species, and it is precisely on the *utility of Specific Differences that the students of Adaptation are* silent. For, as Darwin and many others have often pointed out, the characters which visibly differentiate species are not as a rule capital facts in the constitution of vital organs, but more often they are just those features which seem to us useless and trivial, such as the patterns of scales, the details of sculpture on chitin or shells, differences in number of hairs or spines, differences between the sexual prehensile organs, and so forth. These differences are often complex and are strikingly constant, but their utility is in almost every case problematical. For example, many suggestions have been made as to the benefits which edible moths may derive from their protective coloration, and as to the reasons why unpalatable butterflies in general are brightly coloured; but as to the *particular benefit which one dull moth enjoys as the result of his own* particular pattern of dullness as compared with the closely similar pattern of the next species, no suggestion is made. Nevertheless these are exactly the real difficulties which beset the utilitarian view of the building up of Species. We knew all along that Species are *approximately* adapted to their circumstances; but the difficulty is that whereas the differences in adaptation seem to us to be approximate, the differences between the structures of species are frequently precise. In the early days of the Theory of Natural Selection it was hoped that with searching the direct utility of such small differences would be found, but time has been running now and the hope is unfulfilled.

Even as to the results which rank among the triumphant successes of this method of study there is need for great reserve. The adequacy of such evidence must necessarily be a matter for individual judgment, but in dealing with questions of Adaptation more than usual caution is needed. No disrespect is intended towards those who have sought to increase our acquaintance with these obscure phenomena; but since at the present time the conclusions arrived at in this field are being allowed to pass unchallenged to a place among the traditional beliefs of Science, it is well to remember that the evidence for these beliefs is far from being of the nature of proof.

The real objection however to the employment of the Study of Adaptation as a means of discovering the processes of Evolution is not that its results are meagre and its conclusions unsound. Apart from the doubtful character of these inferences, there is a difficulty of logic which in this method is inherent and insuperable. This difficulty lies in the fact that while it is generally possible to suggest some way by which in circumstances, known or hypothetical, any given structure may be of use to any animal, it cannot on the other hand ever be possible to prove that such structures are not on the whole harmful either in a way indicated or otherwise. There is a special reason why the impossibility of proving the negative applies with peculiar force to the mode of reasoning we are now considering. This is due to the fact that whereas the only possible test of the utility of a structure must be a quantitative one, such a quantitative method of assessment is entirely beyond our powers and is likely to remain so indefinitely. The students of Adaptation forget that even on the strictest application of the theory of Selection it is unnecessary to suppose that every part an animal has, and every thing which it does, is useful and for its good. We, animals, live not only by virtue of, but also in spite of what we are. It is obvious from inspection that any instinct or any organ *may* be of use: the real question we have to consider is of *how much* use it is. To know that the presence of a certain organ *may* lead to the preservation of a race is useless if we cannot tell how much preservation it can effect, how many individuals it can save that would otherwise be lost; unless we know also the degree to which its presence is harmful; unless, in fact, we know how its presence affects the profit and loss account of the organism. We have no right to consider the utility of a structure *demonstrated*, in the sense that we may use this demonstration as evidence of the causes which have led to the existence of the structure, until we have this quantitative knowledge of its utility and are able to set off against it the cost of the production of the structure and all the difficulties which its presence entails on the organism. No one who has ever tried to realize the complexity of the relations between an organism and its surroundings, the infinite variety of the consequences which every detail of structure and every shade of instinct *may* entail upon the organism, the precision of the correlation between function and the need for it, and above all the marvellous accuracy with which the presence or absence of a power or a structure is often compensated among living beings—no one can reflect upon these things and be hopeful that our quantitative estimates of utility are likely to be correct. But in the absence of such correct and final estimates of utility, we must never use the *utility* of a structure as a point of departure in considering the manner of its origin; for though we can see that it is, or may be, useful, yet a little reflexion will shew that it is, or may be, harmful, but whether on the whole it is useful or on the whole harmful, can only be guessed at. It thus happens that we can only get an indefinite knowledge of Adaptation, which for the purposes of our problem is not an advance beyond the original knowledge that organisms are all *more or less* adapted to their circumstances. No amount of evidence of the same kind will carry us beyond this point. Hence, though the Study of Adaptation will always remain a fascinating branch of Natural History, it is not and cannot be a means of directly solving the problem of the origin of Species.

SECTION III.

Continuity or Discontinuity of Variation.

What is needed, then, is evidence of a new kind, for no amount of evidence of the kinds that have been mentioned will take us much beyond our present position. We need more knowledge, not so much of the facts of anatomy or development, as of the principles of Evolution. The question to be considered is how such knowledge may be obtained. It is submitted that the Study of Variation gives us a chance, and perhaps the only one, of arriving at this knowledge.

But though, as all will admit, a knowledge of Variation lies at the root of all biological progress, no organized attempt to obtain it has been made. The reason for this is not very clear, but it apparently proceeds chiefly from the belief that the subject is too difficult and complex to be a profitable field for study. However this may be, the fact remains, that since the first brief treatment of the matter in *Animals and Plants under Domestication* no serious effort to perceive or formulate principles of Variation has been made, and there is before us nothing but the most meagre and superficial account of a few of its phenomena. Darwin's first collection of the facts of Variation has scarcely been increased. These same facts have been arranged and rearranged by each successive interpreter; the most various and contradictory propositions have been established upon them, and they have been strained to shew all that it can possibly be hoped that they will shew. Any one who cares to glance at the works of those who have followed Darwin in these fields may assure himself of this. So far, indeed, are the interpreters of Evolution from adding to this store of facts, that in their hands the original stock becomes even less until only the most striking remain. It is wearisome to watch the persistence with which these are revived for the purpose of each new theorist. How well we know the offspring of Lord Morton's mare, the bitch 'Sappho,' the Sebright Bantams, the Himalaya Rabbit with pink eyes, the white Cats with their blue eyes, and the rest! Perhaps the time has come when even these splendid observations cannot be made to shew much more. Surely their use is now rather to point the direction in which we must go for more facts.

The questions which by the Study of Variation we hope to answer may be thus expressed. In affirming our belief in the doctrine of the Community of Descent of living things, we declare that we believe all living things to stand to each other in definite genetic relationships. If then all the individuals which have lived on the earth could be simultaneously before us, we believe that it would be possible to arrange them all, so that each stood in its own ordinal position in series. We believe that all the secondary series together make up one primary series from which each severally arises. This is the fundamental conception of Evolution and is represented figuratively by the familiar image of a genealogical tree. If then all the individual ancestors of any given form were before us and were arranged in their order, we believe they would constitute a series. This view of the forms of organisms as constituting a series or *progression* is the central idea of modern biology, and must be borne continually in mind in the attempt to apply any principle to the Study of Evolution.

Each individual and each type which exists at the present moment stands, for the moment, therefore, as the last term of such a series. The problem is to find the other terms. In the case of each type the question is thus stated in a particular form, and it is a somewhat remarkable circumstance that it is in its particular forms that this problem has been most studied. The same problem is nevertheless capable of being stated in the general form also. Instead of considering what has been the actual series from which a specified type has been derived, we may consider what are the characters and attributes of such series in general. It may indeed be contended that it is scarcely reasonable to expect to discover the line of descent of a given form, for the evidence is gone; but we may hope to find the general charararacteristics of Evolution, for Evolution, as we believe, is still in progress. It is really a strange thing that so much enterprise and research should have been given to the task of reconstructing particular pedigrees—a work in which at best the facts must be eked out largely with speculation—while no one has ever seriously tried to determine the general characters of such a series. Yet if our modern conception of Descent is a right one, it is a phenomenon now at this time occurring, which by common observations, without the use of any imagination whatever, we may now see. The chief object, then, with which we shall begin the Study of Variation will be the determination of the nature of the Series by which forms are evolved.

The first questions that we shall seek to answer refer to the manner in which differentiation is introduced in these Series.

All we as yet know is the last term of the Series. By the postulate of Common Descent we take it that the first term differed widely from the last, which nevertheless is its lineal descendant: how then was the transition from the first term to the last term effected? If the whole series were before us, should we find that this transition had been brought about by very minute and insensible differences between successive terms in the Series, or should we find distinct and palpable gaps in the Series? In proportion as the transition from term to term is minimal and imperceptible we may speak of the Series as being **Continuous,** while in proportion as there appear in it lacunae, filled by no transitional form, we may describe it as **Discontinuous.** The several possibilities may be stated somewhat as follows. The Series may be wholly continuous; on the other hand it may be sometimes continuous and sometimes discontinuous; we know however by common knowledge that it is never wholly discontinuous. It may be that through long periods of the Series the differences between each member and its immediate predecessor and successor are impalpable, while at certain moments the series is interrupted by breaches of continuity which divide it into groups, of which the composing members are alike, though the successive groups are unlike. Lastly, discontinuity may occur in the evolution of particular organs or particular instincts, while the changes in other structures and systems may be effected continuously. To decide which of these agrees most nearly with the observed phenomena of Variation is the first question which we hope, by the Study of Variation, to answer. The answer to this question is of vital consequence to progress in the Study of Life.

The preliminary question, then, of the degree of continuity with which the process of Evolution occurs, has never been decided. In the absence of such a decision there has nevertheless been a common assumption, either tacit or expressed, that the process is a continuous one. The immense consequence of a knowledge of the truth as to this will appear from a consideration of the gratuitous difficulties which have been introduced by this assumption. Chief among these is the difficulty which has been raised in connexion with the building up of new organs in their initial and imperfect stages, the mode of transformation of organs, and, generally, the Selection and perpetuation of minute variations. Assuming then that variations are minute, we are met by this familiar difficulty. We know that certain devices and mechanisms are useful to their possessors; but from our knowledge of Natural History we are led to think that their usefulness is consequent on the degree of perfection in which they exist, and that if they were at all imperfect, they would not be useful. Now it is clear that in any continuous process of Evolution such stages of imperfection must occur, and the objection has been raised that Natural Selection cannot protect such imperfect mechanisms so as to lift them into perfection. Of the objections which have been brought against the Theory of Natural Selection this is by far the most serious.

The same objection may be expressed in a form which is more correct and comprehensive. We have seen that the differences between Species on the whole are Specific, and are differences of kind, forming a discontinuous Series, while the diversities of environment to which they are subject are on the whole differences of degree, and form a continuous Series; it is therefore hard to see how the environmental differences can thus be in any sense the directing cause of Specific differences, which by the Theory of Natural Selection they should be. This objection of course includes that of the utility of minimal Variations.

Now the strength of this objection lies wholly in the supposed continuity of the process of Variation. We see all organized nature arranged in a discontinuous series of groups differing from each other by differences which are Specific; on the other hand we see the divers environments to which these forms are subject passing insensibly into each other. We must admit, then, that if the steps by which the divers forms of life have varied from each other have been insensible—if in fact the forms ever made up a continuous series—these forms cannot have been broken into a discontinuous series of groups by a continuous environment, whether acting directly as Lamarck would have, or as selective agent as Darwin would have. This supposition has been generally made and admitted, but in the absence of evidence as to Variation it is nevertheless a gratuitous assumption, and as a matter of fact when the evidence as to Variation is studied, it will be found to be in great measure unfounded.

In what follows so much will be said of discontinuity in Variation that it will not be amiss to speak of the reasons which have led many to suppose that the continuity of Variation needs no proof. Of these reasons there are especially two. First there is in the minds of some persons an inherent conviction that *all* natural processes are continuous. That many of them do not appear so is admitted: it is admitted, for example, that among chemical processes Discontinuity is the rule; that changes in the states of matter are commonly effected discontinuously, and the like. Nevertheless it is believed that such outward and visible Discontinuity is but a semblance or mask which conceals a real process which is continuous and which by more searching may be found. With this class of objections we are not perhaps concerned, but they are felt by so many that their existence must not be forgotten. Secondly, Variation has been supposed to be always continuous and to proceed by minute steps because changes of this kind are so common in Variation. Hence it has been inferred that the mode of Variation thus commonly observed is universal. That this inference is a wrong one, the facts will shew.

To sum up:

The first question which the Study of Variation may be expected to answer, relates to the origin of that Discontinuity of which Species is the objective expression. Such Discontinuity is not in the environment; may it not, then, be in the living thing itself?

The Study of Variation thus offers a means whereby we may hope to see the processes of Evolution. We know much of what these processes *may* be: the deductive method has been tried, with what success we know. It is time now to try if these things cannot be seen as they are, and this is what Variation may shew us. In Variation we look to see Evolution rolling out before our eyes. In this we may fail wholly and must fail largely, but it is still the best chance left.

SECTION IV.

SYMMETRY AND MERISTIC REPETITION.

Having thus indicated some of the objects which we may hope to reach by the Study of Variation, we have next to consider the way in which to set about this study.

The Study of Variation is essentially a study of differences between organisms, so for each observation of Variation at least two substantive organisms are required for comparison. It is proposed to confine the present treatment of the subject to a consideration of the integral steps by which Variation may proceed; hence it is desirable that the two organisms compared should be parent and offspring, and if, as is often the case, the actual parent is unknown, it is at least necessary that the normal form of the species should be known and that there must be reasonable evidence that the varying offspring is actually descended from such a normal. For this reason, evidence from a comparison of Local Races, and other established Varieties, though a very valuable part of the Study, will for the most part not be here introduced. For the belief that such races are descended from the putative normal scarcely ever rests on proof, and still more rarely is there evidence of the number of generations in which the change has been effected.

For our purpose we require actual cases of Variations occurring as far as possible in offspring of known parentage; and if, failing this, we make use of cases occurring in the midst of normal individuals of known structure, it must in such cases be always remembered that we cannot properly assume that the varying form is the offspring of such individuals, though special reasons may make this likely in special cases.

Since the structure of the offspring is perhaps in no case identical with that of the parent, observation of any parent and its offspring is to the point; but such a field as this is plainly too wide to be studied with profit as a whole, and it is necessary from the first, that attention should be limited to certain classes of such phenomena. With this object certain limitations are proposed, and though confessedly arbitrary, they will be found on the whole to work well.

The first limitation thus introduced concerns the *magnitude* of Variations. We have seen above that the assumption that Variation is a continuous process lands us in serious difficulties in the application of a hypothesis which, on general grounds, we nevertheless are prepared to receive. If then we can shew that Variation is to some extent discontinuous, a road will be opened by which these difficulties may perhaps be in part avoided.

Species are discontinuous; may not the Variation by which Species are produced be discontinuous too? It may be stated at once that evidence of such Discontinuous Variation does exist, and in this first consideration of the subject attention will be confined to it. The fact that Continuous Variation exists is also none the less a fact, but it is most important that the two classes of phenomena should be recognized as distinct, for there is reason to think that they are distinct essentially, and that though both may occur simultaneously and in conjunction, yet they are manifestations of distinct processes. The attempt to distinguish these two kinds of Variation from each other constitutes one of the chief parts of the study. It will not perhaps be possible to find any general expression which shall accurately differentiate between Variations which are Discontinuous and those which are Continuous, but it is possible to recognize attributes proper to each and to distinguish changes which are or may be effected in the one way from other changes which are or may be effected in the other.

For the present we shall treat only of the evidence of Discontinuous Variation.

In order to explain the second limitation which is to be introduced it is necessary to refer to some phenomena which are characteristic of the forms of organisms, and to separate from them the group with which we shall deal first.

It was stated above that perhaps no character of form is common to all living things, but nevertheless there is one feature which is found in the great majority.

In the first place, the bodies of organisms are not homogeneous but heterogeneous, consisting of organs or parts which in substance and composition differ from each other. This heterogeneity in composition is of course an objective expression of the process of Differentiation, and it is further recognized that such structural heterogeneity of material corresponds with a physiological Differentiation of function. This Differentiation or Heterogeneity is found in the bodies of all organisms, even in the simplest.

Now in a wide survey of the forms of living things there is a fact with regard to the presence of this Heterogeneity which to the purpose of our present consideration is of the highest consequence. This may perhaps be best expressed by the statement that in the bodies of living things Heterogeneity is generally orderly and formal; it is cosmic, not chaotic. Not only are the bodies of all organisms heterogeneous, but in the great majority the Heterogeneity occurs in a particular way and according to geometrical rule. This character is not peculiar to a few organisms, but is common to nearly all. We will now examine this phenomenon of geometrical order in Heterogeneity and try to see some of the elements of which it is made up.

Order of form will first be found to appear in the fact that in any living body the Heterogeneity is in some degree symmetrically distributed around one or more centres. In the great majority of instances these centres of symmetry are themselves distributed about other centres, so that in one or more planes the whole body is symmetrical.

The idea of **Symmetry** which is here introduced is so familiar that it is scarcely necessary to define it, but as all that follows depends entirely on the proper apprehension of what is meant by Symmetry it may be well to call attention to some of the phenomena which the term denotes.

In its simplest form the Symmetry of a figure depends on the fact that from some point within it at least two lines may be taken in such a way that each passes through parts which are similar and similarly disposed. The point from which the lines are taken may be called a centre of Symmetry and the lines may be called lines of Symmetrical Repetition.

Commonly the parts thus symmetrically disposed are related to each other as optical images [in a plane mirror passing through the centre of Symmetry and standing in a plane bisecting the angle which the lines of Symmetrical Repetition make with each other]. For a figure to be symmetrical, in the ordinary sense of the term, it is not necessary that the relation of optical images should strictly exist, and several figures, such as spirals, &c., are accordingly described as symmetrical. But since the relation of images exists in all cases of bilateral and radial symmetry, which are the forms most generally assumed in the symmetry of organisms, it is of importance to refer particularly to this as one of the phenomena often associated with Symmetry.

In the simplest possible case of Symmetry there is a series of parts in one direction corresponding to a series of parts in another direction. Perhaps there is no organism in which such an arrangement does not at some time and in some degree exist. For even in an unsegmented ovum or a resting *Amœba* there is little doubt that Symmetry is present, though owing to the slight degree of Differentiation, its presence may not be clearly perceived. In the manifestations, however, in which it is most familiar, Symmetry is a decided and obvious phenomenon.

Symmetry then depends essentially on the fact that structures found in one part of an organism are repeated and occur again in another part of the same organism. Symmetrical Heterogeneity may therefore be present in a spherical body having a core of different material, and it is possible that in an unsegmented ovum for example a Symmetry of this simple kind may exist. But Symmetry, as it is generally seen in organisms, differs from that of these simplest cases in the fact that the organs repeated are separated from each other by material of a nature different from that of the organs separated. Repetitions of this kind are known in almost every group of animals and plants. The parts thus separated may belong to any system of organs. There is no known limit to the number of Repetitions that may occur.

This phenomenon of Repetition of Parts, generally occurring in such a way as to form a Symmetry or Pattern, comes near to being a universal character of the bodies of living things. It will in cases which follow be often convenient to employ a single term to denote this phenomenon wherever and however occurring. For this purpose the term **Merism** will be used. The introduction of a new term is, as a practice, hardly to be justified; but in a case like the present, in which it is sought to associate divers phenomena which are commonly treated as distinct, the employment of a single word, though a new one, is the readiest way of giving emphasis to the essential unity of the phenomena comprised.

The existence of patterns in organisms is thus a central fact of morphology, and their presence is one of the most familiar characters of living things. Anyone who has ever collected fossils, or indeed animals or plants of any kind, knows how in hunting, the eye is caught by the formal regularity of an organized being, which, contrasting with the irregularity of the ground, is often the first indication of its presence. Though of course not diagnostic of living things, the presence of patterns is one of their most general characters.

On examining more closely into the constitution of Repetitions, they may be seen to occur in two ways; first, by Differentiation within the limits of a single cell, as in the *Radiolaria*, the sculpture of egg-shells, nuclear spindles, &c., to take marked cases; and secondly, by, or in conjunction with, the process of Cell-Division. The Symmetry which is found in the Serial Repetitions of Parts in unicellular organisms does not in all probability differ essentially from that which is produced by Cell-Division, for, though sufficiently distinct in outward appearance, the two are almost certainly manifestations of the same power.

Such patterns may exist in single cells or in groups of cells, in separate organs or in groups of organs, in solitary forms or in colonies and groups of forms. Patterns which are completed in the several organs or parts will be referred to as **Minor Symmetries.** These may be compounded together into one single pattern, which includes the whole body: such a symmetry will be called a **Major Symmetry.** In most organisms, whether colonial or solitary, there is such a Major Symmetry; on the other hand organisms are known in which each system of Minor Symmetry is, at least in appearance, distinct and without any visible geometrical relation to the other Minor Symmetries. Examples of this kind are not common, for, as a rule, the planes about which each Minor Symmetry is developed have definite geometrical relations to those of the other Minor Symmetries. It is possible, even, that in some if not all of these, the planes of division by which the tissues composing each system of Minor Symmetry are originally split off and differentiated, have such definite relations, though by subsequent irregularities of growth and movement these relations are afterwards obscured.

The classification of Symmetry and Pattern need not now be further pursued. The matter will be often referred to in the course of this work, when facts concerning Variations in number and patterns are being given, for it is by study of Variations in pattern and in repetition of parts that glimpses of the essential phenomena of Symmetry may be gained.

That which is important at this stage is to note the almost universal presence of Symmetry and of Repetition of Parts among living things. Both are the almost invariable companions of division and differentiation, which are fundamental characters without which Life is not known.

The essential unity of the phenomenon of Repetition of Parts and of its companion-phenomenon, Symmetry, wherever met with, has been too little recognized, and needless difficulty has thus been introduced into morphology. To obtain a grasp of the nature of animal and vegetable forms, such recognition is of the first consequence.

To anyone who is accustomed to handle animals or plants, and who asks himself habitually—as every Naturalist must—how they have come to be what they are, the question of the origin and meaning of patterns in organisms will be familiar enough. They are the outward and visible expression of that order and completeness which inseparably belongs to the phenomenon of Life.

If anyone will take into his hand some complex piece of living structure, a Passion-flower, a Peacock's feather, a Cockle-shell, or the like, and will ask himself, as I have said, how it has come to be so, the part of the answer that he will find it hardest to give, is that which relates to the perfection of its pattern.

And it is not only in these large and tangible structures that the question arises, for the same challenge is presented in the most *minute and seemingly trifling details. In the skeleton of a Diatom* or of a Radiolarian, the scale of a Butterfly, the sculpture on a pollen-grain or on an egg-shell, in the wreaths and stars of nuclear division, such patterns again and again recur, and again and again the question of their significance goes unanswered. There are many suggestions, some plausible enough, as to why the tail *of a Peacock is gaudy, why the coat of a pollen-grain should be* rough, and so forth, but the significance of patterns is untouched by these. Nevertheless, repetitions arranged in pattern exist throughout organized Nature, in creatures that move and in those that are fixed, in the great and in the small, in the seen and in the hidden, within and without, as a property or attribute of Life, *scarcely less universal than the function of respiration or metabolism* itself.

Such, then, is Symmetry, a character whose presence among organisms approaches to universality.

SECTION V.

Meristic Variation and Substantive Variation.

It is to the origin and nature of Symmetry that the first *section of the evidence of Variation will relate.* That a knowledge of the modes of Variation of so universal a character is important to the general study of Biology must at once be evident, but to the particular problem of the nature of Specific Differences this importance is immense. This special importance comes from two reasons. As it is the fact first that Repetition and Symmetry are *among the commonest features of organized structure,* so it will be found next that it is by differences in those features that the various forms of organisms are very commonly differentiated from each other. Their forms are classified by all sorts of characters, by shape and proportions, by size, by colour, by habits and the like; but perhaps almost as frequently as by any of these, by differences in number of parts and by differences in the geometrical relations of the parts. It is by such differences that the larger divisions, genera, families, &c. are especially distinguished. In such cases of course the differences in number and Symmetry do not as a rule stand alone, but are generally, and perhaps always, accompanied by other differences of a qualitative kind; nevertheless, the differences in number and Symmetry form an integral and very definite part of the total differences, so that in any consideration of the nature of the processes by which the differences have arisen, special regard must be had to these numerical and geometrical, or, as I propose to call them, **Meristic**, changes.

In the present Introduction I do not propose to forestall the evidence more than is absolutely necessary for the purpose of making clear the principles on which the facts are grouped, but it will do the evidence no wrong if at the present stage it is stated that Meristic Variation is frequently Discontinuous, and that in the case of certain classes of Repetitions is perhaps always so.

The nature of Merism and the manner in which Meristic Variations occur will be fully illustrated hereafter, but it is necessary to say this much at the present stage, since it is from *this Discontinuity in the occurrence of Meristic Variations that* the phenomena of Symmetry and Repetition derive their special importance in the Study of Variation.

The importance of the phenomena of Merism to the Study of Variation is thus, in the first instance, a direct one, for the Variations which have resulted in the production of Meristic Systems are a direct factor in Evolution. In addition to this direct relation to the Study of Variation, the phenomena of Merism have also an indirect relation, which is scarcely less important; for they are a factor in the estimation of the magnitude of the integral steps by which Variation proceeds. This will be more evident after the second group of Variations has been spoken of.

We have thus far spoken only of the processes by which the living body is divided into parts, and we have thus constituted a group which is to include Variations in number, Division, and geometrical position. From these phenomena of Division may be distinguished Variations in the actual constitution or substance of the parts themselves. To these Variations the name **Substantive** will be given. Under this head several phenomena may be temporarily grouped together, which with further knowledge will doubtless be found to have no real connexion with each other. For the present, however, it will be convenient to constitute such a temporary group in order to bring out the relative distinctness of Variations which are Meristic.

These two classes of Variation, Meristic and Substantive, may be recognized at the outset of the study. There can be no doubt that they are essentially distinct from each other, and the proof that they are thus distinct will be found in the evidence of Variation, for it will be seen that either may occur independently of the other. An appreciation of this distinction is a first step towards a comprehension of the processes by which the bodies of organisms are evolved.

A few simple illustrations may make the nature of these two classes of Variations more clear. For example, then, the flower of a *Narcissus* is commonly divided into six parts, but through Meristic Variation it may be divided into seven parts or into only four. Nevertheless there is in such a case no perceptible change in the tissues or substance of which the parts are made up. All belong to and are recognizable as belonging to the same sort of *Narcissus*. On the other hand many *Narcissi, N. corbularia*, for example, are known in two colours, one a dark yellow and the other a sulphur-yellow, though the number of parts and pattern of the flowers are identical. This is, therefore, an example of a Substantive Variation.

Again, the foot of a Pig may, through Meristic Variation, be divided into five or six toes instead of into four; or, on the other hand, the number may, by absence of the median division between the digits III and IV, be reduced to three, though the tissues composing the toes may not in structure differ from the normal.

Again, the tarsus of a Cockroach (*Blatta*) may, through Meristic Variation, be divided into only four joints instead of into five, the normal number, but the joints are still in substance or quality those of a Cockroach.

I am aware that Meristic and Substantive Variations often occur together, and that there is a point at which it is not possible to separate satisfactorily the changes which have come about by the one process from those which have come about by the other. Instances of this kind occur especially in the case of series of parts such as Teeth or Vertebræ, in which individual members or groups of members of the series are differentiated from the others. For example, we may see that it is through Meristic Variation that the vertebral column of a Dog may be divided into a number of Vertebræ greater or less than the normal; and though in such cases all the Vertebræ have distinctively canine characters, yet there are nearly always Substantive Variations occurring in correlation with the Meristic Variations, manifesting themselves in a re-arrangement of the points of division between the several groups of Vertebræ, and causing individual Vertebræ to assume characters which are not proper to their ordinal positions.

Further inquiry into the questions thus raised cannot at this stage be profitably undertaken, though when the evidence has been considered it will perhaps be advisable to recur to them; all that is now intended is to indicate broadly the general scope of Meristic and Substantive Variation respectively.

As has already been stated, it is proposed to begin the Study of Variation by an examination of Variations which are Meristic, leaving the consideration of Substantive Variation to be undertaken hereafter. But nevertheless in the consideration of Meristic Variation it will be necessary to refer to phenomena of Substantive Variation in so far as their occurrence or distribution in the body are affected by Meristic phenomena. For in the determination of the magnitude of the integral steps by which Variation proceeds, the existence of Merism plays a conspicuous part, and it is in consequence of this that the subject of Symmetry and Repetition of Parts has a second and indirect bearing on the Study of Variation which is scarcely less important than the direct bearing of which mention has been made above.

This indirect bearing on the manner of origin of Specific Differences arises from a circumstance which in treatises on Evolution is commonly overlooked. In comparing a species in which parts are repeated, with an allied species in which the same parts are repeated, it commonly occurs that each of the repeated parts of the one have some character by which they are distinguished from the like parts of the other. This differentiating character may be a qualitative one, or a numerical one, or both. In such cases it very frequently happens that this character occurs in each member of the series of Repetitions. For example, the tarsi of the Weevils have only four visible joints, while those of the majority of beetles have five; but the characteristic division into four joints occurs in each of the legs. Before the four-jointed character as seen in the Weevils could be produced it was necessary that not one but all of the legs should vary from the five-jointed form, and in this particular way. The leaves on a beech tree are all beech leaves, and if the tree is a fern-leaved beech, they *may*, and generally speaking do, all shew the characters of that variety; and so on with other particular species and varieties.

The limbs of a bilaterally symmetrical animal, in which the right side is the image of the left, are of course alike, and any specific character which is present in the limbs of the one side must in such an animal be normally present in those of the other side.

The same is true of many forms in which appendages are repeated in series, as for example, the fore-legs and hind-legs of the Horse, the fore- and hind-wings of the Brimstone Butterfly (*Gonepteryx rhamni*); of the patterns on several segments of many caterpillars; of the patterns of the segmental setæ of many worms, and so forth. In series whose members are differentiated from each other, it of course frequently happens that the same specific characters are not present in all the members of the series, and in nearly all such cases these characters are not presented by all in equal degree; nevertheless substantially the phenomenon remains that similar characters often are presented by the several members of a series of repeated organs.

To many this will seem little better than a truism, nevertheless I offer no apology for its introduction; for though, as a common and obvious fact, it is a truism, it is besides a truth, the far-reaching significance of which is scarcely appreciated. For, in the consideration of the magnitude of the integral steps by which Variation proceeds, we shall have this to remember: that to produce any of the forms of which we have spoken, by Variation from another form, it is not enough that the particular Variation should occur and become fixed in one member of the series, but it is necessary that the character should sooner or later be taken on by *each* member of the series which exhibits it. In such cases therefore, this question is raised. Did the Variation come in first in one member of the Series and then in another? Did it occur, for example, simultaneously on the two sides of the body? Did the right and left fore-legs of the Horse cease to develop more than the present number of digits simultaneously or separately? Was the similar form of the hind-legs assumed before, after, or simultaneously with that of the fore-legs? Were the orange markings which are present on both fore- and hind-wings of the Brimstone, or the ocellar markings of the Peacock (*V. Io*), and of the Emperor (*Saturnia carpini*), assumed by both wings at once? Were the four wings of the Plume Moths split simultaneously into the characteristic "plumes"? Did the brown spots on the three leaflets of *Medicago*, the fimbriation of the petals of Ragged Robin (*Lychnis flos-cuculi*), the series of stripes on the Zebra, the pink slashes on the segments of *Sphinx* larvae, the eyes on the scutes of Chitons, and the thousand other colour-marks, sense-organs, appendages and structural features, which throughout organized Nature occur in Series, vary to their present state of similarity by similar and simultaneous steps, or did each member of such Series take these characters by steps which were separate and occurring independently? To this question, which lies at the root of all progress in the knowledge of Evolution, the Study of Variation can alone reply. That in the facts which follow, the answer to this question will be found, cannot of course be said; but these facts, few though they are, do nevertheless answer it in part, and they suggest that more facts of the same kind would go far towards answering it completely. But beyond this, the facts are of value as an indication of the part which the phenomenon of Merism may play in determining the magnitude of Variations and the manner of their distribution among the several parts of the body. On examining the evidence it will be found that between parts related to each other in the way that has been described, there is a certain bond or kinship, by virtue of which they *may* and often do vary simultaneously and in similar ways, though the fact that they may also vary independently, and in different ways, will of course also appear.

The phenomenon of the Similar Variation of parts which are repeated Meristically in Series is a fact which will be found to have important bearings on several distinct departments of biological study.

As was shewn above, it is by recognition of the existence of such similar and simultaneous Variation that the manner of origin of the similar complexity of several organs belonging to the same system or series becomes comparatively comprehensible; for it is not then necessary to conceive a separate origin for the complexity of each member of the series. For example, it is difficult to conceive the manner of evolution of an eye of a vertebrate; nevertheless, for each vertebrate *two* eyes have been evolved. If it were necessary to suppose that each arose by separate selections of separate variations, the difficulty would be thus doubled. If, however, it is recognized that the complexity of both arose simultaneously, the phenomenon becomes the more intelligible as the number of integral variations and selections demanded is reduced.

The case chosen, of paired organs in bilateral symmetry, is a very simple one, but it will be found that similar relations hold between other parts repeated in series. For in the same way it is not necessary to suppose an independent evolution for each of the tail-feathers of the Peacock, for the legs of the Horse, and the like, since in the light of the facts of Variation it is as easy for all to take on the new characters as for one.

If the manner of development of Repeated Parts is considered, this fact will not seem surprising. For all these parts arise from *the undifferentiated tissues by a process of Division, and whatever* characters were potentially present in the undifferentiated tissues may appear in the parts into which it subsequently divides. A somewhat loose illustration will perhaps make this more clear. Everyone knows the rows of figures which children cut out from folded paper. There are as many figures as folds, each figure being alike if the folds coincide. If the paper is pink, all the figures are pink; if the paper is white, all the figures are white, and so on. If blotting-paper is used, and one blot is dropped on the folded edges, the blot appears symmetrically in all the figures. So also any deviation in the lines of cutting appear in all the figures; a whole row of soldiers in bearskins may be put into helmets by one stroke of the scissors. Of course it is not meant to suggest that the process of division by which parts of the body are produced bears any resemblance to that by which the figures are cut out, but merely to illustrate the fact that since it is by a process *of Division of an undifferentiated mass that the* Repeated Parts are produced, so the characters of these Repeated Parts depend upon the characters which were present in the original mass and upon the modes by which the parts were divided out from it.

Summary of Sections I to V.

At this point it will be well briefly to recapitulate the preceding Sections.

We are proposing to attack the problem of Species by studying the facts of Variation. Of the facts of Variation in general we have selected a particular group upon which to begin this study. The group of variations thus chosen are those which relate to Number of parts, Division, Repetition, and the other phenomena which are to be included under the term Meristic. With variations in quality and Substance it is not at present proposed to deal, except in so far as it is necessary to refer to them in their relation to the phenomena of Merism, and in illustration of the structural possibilities or necessities which in the body follow as corollaries upon the existence of Meristic Repetition.

It has also been proposed to limit the consideration to Variations which are Discontinuous. As has been already stated, Discontinuous Variations may belong to the Meristic Group or to the Substantive, but it is to the former that attention will first be directed.

SECTION VI.

MERISTIC REPETITION AND HOMOLOGY.

In what has gone before, the two conceptions now introduced, namely the distinction of Variations into Meristic and Substantive, and into Continuous and Discontinuous, have been sketched in outline. The significance of the facts which follow will be made more evident if these two conceptions are now more fully developed in some of their aspects.

Under the name Merism I have proposed to include all phenomena of Repetition and Division, whenever found and in whatever forms occurring, whether in the parts of a body or in the whole. The consequences of the admission of this proposition are considerable and should be fully realized; for on recognition of the unity of these phenomena it is possible to group together a number of facts whose association will lead to simplification of some morphological conceptions, and to other results of utility.

That the phenomena of Merism form a natural group is in some respects a familiar idea, but in its fullest expression it is as yet not generally received, still less have the consequences which it entails been properly appreciated. Every one who has gone even a little way into morphological inquiry has met some of the difficulties to which we shall now refer.

It is with respect to the phenomena of Segmentation that these difficulties are most familiar, and it is in this connexion that they may be best discussed. Segmentation is a condition which reaches its highest development in Vertebrates, the Annelids, and the Arthropods, and it is in these groups that it has been most studied. In them it appears as a more or less coincident Repetition of elements belonging to most of the chief systems of organs along an axis corresponding to the long axis of the body. To segmentation of this kind the name 'Metameric' has been given, and by many morphologists the attempt has been made, either tacitly or in words, to separate such Metameric Segmentation from other phenomena of Repetition elsewhere occurring.

It has thus been attempted to distinguish the Repetitions which occur along the long axis of the body from those occurring along the long axis of appendages, such as for example the joints of antennæ or of digits, and some have even gone so far as to regard the Segmentation of the Vertebrate tail as a thing different in kind from that of the trunk itself. It would be apart from our present purpose to recur to these subjects, were it not that this suggestion of the existence of a difference in kind between Metameric Segmentation and other Repetitions has led to several notable errors in the interpretation of the facts of morphology and in the application of these facts to the solution of the problems of Descent. In order to lay a sound foundation for the study of Meristic Variation these errors must be cleared away, and to do this it is necessary to break down the artificial distinction between the phenomena of Metameric Segmentation and other cases of Repetition of Parts, so that the whole may be seen in their true relations to each other. When this is done, the mutual relations of the facts of Meristic Variation will also become more evident.

The first difficulty which has been brought into morphology by the suggestion that Metameric Segmentation is a phenomenon distinct in kind, is one which has coloured nearly all reasoning from the facts of Morphology to problems of phylogeny. For the existence of Metameric Segmentation in any given form is thus taken to be one of its chief characters, and, as such, is allowed predominant weight in considering the genetic relations of these forms. By the indiscriminate though logical extension of this principle the conclusion has been reached that Vertebrates are immediately connected with, or have arisen by Descent from Annelids, or from Crustacea and the like, for the Repetition in these forms is closely similar. Others again, being struck with the resemblance between the Repetition of Parts along the radial axes of Starfishes and those which occur along the long axes of Annelids have hazarded the conjecture that perhaps this resemblance may indicate the actual phylogenetic history of these Repetitions. Though such speculations as these are little better than travesties of legitimate theory, some of them still command interest if not belief.[1] All alike are founded on the assumption that resemblances between the manner and degree in which Repetition occurs are unlikely to have arisen save by community of Descent. A broader view of Meristic phenomena will shew that

[1] These modern "Instances" recall many that once were famous but are now forgotten. For example : *Item non absurda est similitudo et conformitas illa, ut homo sit tanquam planta inversa. Nam radix nervorum et facultatum animalium est caput; partes autem seminales sunt infimæ, non computatis extremitatibus tibiarum et brachiorum. At in planta, radix (quæ instar capitis est) regulariter infimo loco collocatur; semina autem supremo.* BACON, *Nov. Org.* Lib. II. 27. In *non computatis extremitatibus*, amateurs of INSTANTIÆ CONFORMES may still find matter for warning.

this assumption is unfounded; for so far are the expressions of it which are called Metamerism from standing alone, that it is almost impossible to look at any animal or vegetable form without meeting phenomena of Repetition which differ from Metamerism only in degree or in extent. Between these Repetitions and Metameric Repetitions it is impossible to draw any line, and the Meristic Variations of all will therefore be treated together.

This error in the estimate of the value of Metamerism as a guide to phylogeny is one by which the evidence of Variation is only indirectly affected. The other errors now to be mentioned are of a much more serious nature, for they concern the general conception of the nature of Homology which is the basis of all morphological study.

In introducing the method of the Study of Variation I have said that it can alone supply a solid foundation for inquiry into the manner by which one species arises from another. The facts of Variation must therefore be the test of phylogenetic possibility. Looking at organs instead of species, we shall now see that the facts of Variation must also be the test of the way in which organ arises from organ, and that thus Variation is the test of Homology. For the statement that an organ of one form is homologous with an organ of another means that there is between the two some connexion of Descent, and that the one organ has been formed by modification of the other, or both by modification of a third. The precise way in which this connexion exists is not defined, and indeed has scarcely ever been considered, though such a consideration must sooner or later be attempted. We must for the present be content with the belief that in some undefined way there is a relationship between 'homologous' parts, and that this is what we mean when we affirm that they are homologous.

We have however assumed that the transition from one form to another takes place by Variation. If therefore we can see the variations we shall see the precise mode by which the descent is effected, and this must be true of the parts or organs as it is true of the whole body. In like manner then as the Study of Variation may be hoped to shew the way by which one form passes into another, so also may it be hoped that it will shew how the organs of one form take on the shape of the homologous organs of another.

In the absence of the evidence of Variation reasoning as to Homology rests solely on conjecture, and assumptions have thus been made respecting the nature of Homology which have coloured the whole of morphological study. Of these, two demand attention now.

I. *As to Homology between the Members of one Series.* We saw above (page 29) how the resemblance between Repetitions occurring in divers forms has led to the belief that those forms had a common descent: in a somewhat similar way it has happened that the resemblance between individual members of a series of Repeated Parts has led to the belief that they must originally have been alike, and that they have been formed by *differentiation of members originally similar.* Many who would hesitate thus to formulate such a belief nevertheless have taken part in inquiries which can succeed only on the hypothesis that this has been the history of such parts. Of this nature are the old attempts to divide the skull into vertebræ, recognizing the several parts of each; the modern disquisitions on the segmentation of the cranial nerves; the attempts to homologize the several phalanges of the vertebrate pollex and hallux with the several phalanges of the other digits; similar attempts to trace the precise equivalence of the elements of the carpus and tarsus, and many other quests of a like nature. In all these it is assumed that there is a precise equivalence to be found with enough searching, and that all the members of such series of Repetitions were originally alike. If the series of ancestors were before us it is expected that this would be seen to have been the case. In the light of the facts of Variation this assumption will be seen to be a wrong one, and these simple views of the Repetition and Differentiation of members in Series must be given up as inadequate and misleading, even though there be no other to substitute.

II. *As to the individuality of Members of Series.* In seeking to homologize a series of parts in one form with a series of parts in another, cases often occur in which the whole series of the one is admittedly homologous with the whole series of the other. In such cases the question arises, can the principle of Homology be extended to the individual members of the two Series? If the two Series each contain the same number of members this question is a comparatively simple one, for it may be assumed that each member of the Series is the equivalent or Homologue of the member which in the other Series occupies the same ordinal position. If however the number of members differs in the two Series, how is the equivalence to be apportioned? This is a question again and again arising with regard to Meristic Series such as teeth, digits, phalanges, vertebræ, nerves, vessels, mammæ, colour-markings, the parts of the flower, and indeed in almost every system whether of animals or plants. To decide this question there are still no general principles. But though we yet know nothing as to the steps by which Meristic Variation proceeds, there is nevertheless a received view by which the interpretation of the phenomena is attempted, and though in the case of each system of organs the application of the principle is different, yet the principle applied is essentially the same.

Thus to compare the members of Series containing different members it is first assumed that the series consisted ancestrally of some maximum number, from which the formula characteristic of each descendant has been derived by successive diminution. Here, again, I do not doubt that many who employ this assumption would hesitate to make it in set terms, but nevertheless it is the logical basis of all such calculations.

Now this hypothesis involves a definite conception of the mode in which Variation works, and it is most important that this should be realized clearly. For if it is true that each member of a Series has in every form an individual and proper history, it follows that if we had before us the whole line of ancestors from which the form has sprung, we should then be able to see the history of each member in the body of each of its progenitors. In such a Series the rise of an individual member and the decline of another should then be manifest. Each would have its individual history just as a Fellowship in a College or a Canonry in a Cathedral has an individual history, being handed on from one holder to his successor, some being suppressed and others founded, but none being merged into a common fund. In other words, according to the received view of the nature of these homologies, *it is assumed that in Variation the individuality of each member of a Meristic Series is respected.*

The difficulty in applying this principle is notorious, but when the evidence of Variation is before us the cause of the difficulty will become evident. For it will be found that though Variation may sometimes respect individual homologies, yet this is by no means a universal rule; and as a matter of fact in all cases of Meristic Series, as to the Variation of which any considerable body of evidence has been collected, numerous instances of Variation occur, in which what may be called the stereotyped or traditional individuality of the members is superseded.

This error in the application of the principle of Homology to individual members of Meristic Series has arisen almost entirely through want of recognition of the unity of Meristic Repetition, wherever found. In the case of a series of parts among which there is no perceptible Differentiation, no one would propose to look for individual Homologies. For example, no one considers that the individual segments in the intestinal region of the Earthworm have any fixed relations of this kind; no one has proposed to homologize single leaves of one tree with single leaves on another; it is not expected that the separate teeth of a Roach have definite homologies with separate teeth of a Dace, for such expectations would be plainly absurd. But in series whose members are differentiated from each other the existence of such individuality is nevertheless assumed. To take only one case: a whole literature has been devoted to the attempt to determine some point in the vertebral column or in the spinal nerves from which the homologies of the segments may be reckoned. This is a problem which in its several forms has been widely studied. Some have attempted to solve it by starting from the lumbar plexus, while others have begun from the brachial. In the case of Birds this question is reduced to an absurdity. Which vertebra of a Pigeon, which has 15 cervical vertebræ, is homologous with the first dorsal of a Swan which has 26 cervicals? To decide these questions the only possible appeal is to the facts of Variation, and judged by these facts the whole inquiry comes to an end, for it is seen at once that the expectation is founded on a wrong conception of the workings of Variation. No one, as has been said above, would attempt such an inquiry if the series were undifferentiated, for this individuality would not be expected in such a Series; but to suppose that it does exist in a differentiated Series of parts, is to suppose that with Differentiation the ordinal individuality of the members has become fixed beyond revision. This supposition the Study of Variation will dispel.

Here, as in the preceding case of the theoretical doctrine of Serial Homology, the current view is far too simple and far too human. Though the methods of Nature are simple too, yet their simplicity is rarely ours. In these subjective conceptions of Homology and of Variation, we have allowed ourselves to judge too much by human criterions of difficulty, and we have let ourselves fancy that Nature has produced the forms of Life from each other in the ways which we would have used, if we had been asked to do it. If a man were asked to make a wax model of the skeleton of one animal from a wax model of the skeleton of another, he would perhaps set about it by making small additions to and subtractions from its several parts; but the natural process differs in one great essential from this. For in Nature the body of one individual has never *been* the body of its parent, and is not formed by a plastic operation from it; but the new body is made again new from the beginning, just as if the wax model had gone back into the melting-pot before the new model was begun.

SECTION VII.

MERISTIC REPETITION AND DIVISION.

Before ending this preliminary consideration of Merism it is right that we should see other aspects of the matter. What follows is put forward in no sense as theory or doctrine, but simply as suggesting a line of thought which should be in the minds of any who may care to pursue the subject further or to study the evidence. It is perhaps only when it is seen in connexion with its possible developments that the magnitude of the subject can be fully felt.

In the treatises on Comparative Anatomy which belong especially to the beginning of this century, the idea constantly recurs that the series of segments of a metamerically segmented form do in some sort represent a series of individuals which have not detached themselves from each other. Seen in the light of the Doctrine of Descent this resemblance or analogy has been taken as a possible indication that the segmented forms may actually have had some such phylogenetic history as this. By similar reasoning the Metazoa have been spoken of as "Colonies" of Protozoa. Now though we need not allow ourselves to be drawn away into these and other barren speculations as to phylogeny, we may still note the substance of fact which underlies them. For it is now recognized that between the process by which the body of a *Nais* is metamerically segmented, and that by which it divides into a chain of future "individuals," no line can be drawn: that the process of budding, or of strobilization, by which one form gives rise to a number of detached individuals, is often indistinguishable from the process by which a near ally gives rise to a connected colony, and that the two processes may even be interchangeable in the same form; finally that the process of division of a fertilized ovum by the first cleavage plane may be in some essentials comparable with the division of a Protozoon into two new individuals. All these are now commonplaces of Natural History.

With what justice these considerations may have been applied to the problems of phylogeny we need not now inquire, but to the interpretation of the facts of Variation they have an application which ought not to be neglected.

If, then, as is admitted, there is a true analogy between the process by which new organisms may arise asexually by Division, and the process by which ordinary Meristic Series are produced, it follows that Variation, in the sense of difference between offspring and parent, should find an analogy in Differentiation between the members of a Meristic Series. Applied to the case of asexual reproduction there seems no good reason for denying this analogy. It is of course an undoubted fact that in the asexual reproduction of many forms Variation is rare, though the sexually produced offspring of the same forms are very variable. In plants this is familiar to everyone, though the extension of the same principle to animals rests chiefly on inference. Nevertheless in plants bud-variation, both Meristic and Substantive, happens often, and the division of a plant into two dissimilar branches may well be compared to the production of dissimilar offspring by one parent; indeed, if the processes of Division are admitted to be fundamentally the same, this conclusion can scarcely be escaped.

In one more aspect this subject may be considered with profit. It is, as we have seen, believed that the division of an ovum into two segmentation-spheres is not a process essentially different from the division of certain Protozoa into two "individuals." In conceiving the manner of Variation in such Protozoa we have little or no fact to guide us, but this much is obvious: that for the introduction of a variety as the offspring of a given species, it is necessary either that the two parts into which the unicellular organism divided should have varied equally, and that the division should thus be a symmetrical division (in the full sense of qualitative as well as formal symmetry); or that the division should be asymmetrical, the resulting parts being dissimilar, in which case one may conceivably belong to the type and the other be a Variety. If Variation has ever occurred in the reproduction of animals of this class it must have occurred on one or both of these plans.

Returning to the segmentation of the Metazoan ovum we have the well-known results of Roux and others, shewing that, in certain species, the first[1] cleavage-plane divides the body into the future right and left halves. In such cases then on the analogy of the Protozoon, the right and left halves of the body are in a sense comparable with the two young Protozoa, and though each half is hemi-symmetrical, it is in this way the equivalent of a separate organism. This suggestion, which is an old one, receives support from many facts of Meristic Variation, especially from the mode of formation of homologous Twins and "double Monsters" which are now shewn almost beyond doubt, to arise from the division of one ovum[2]. But besides the evidence that each half of the body may on occasion develop into a whole, evidence will be given that one half may vary in its entirety, independently of the other half. Such Variation may be one of sex, taking the form of Gynandromorphy, so well-known among Lepidoptera, in which the secondary sexual characters of one side are male, those of the other being female; or it may happen that the difference between the two sides is one of size, the limbs and organs of one side being smaller than those of the other; or lastly the Variation between the two sides may be one that has been held characteristic of type and variety or even of so-called species and species[3].

These matters have been alluded to here as things which a student of the facts of Variation will do well to bear in mind. It is difficult to see the facts thus grouped without feeling the

[1] *Often it is the second cleavage-plane (if any) which corresponds with the future middle line.*

[2] The well-known evidence relating to this subject will be spoken of later. The view given above, which is now very generally received, finds support in the striking observations of DRIESCH, lately published (*Zt. f. w. Zool.*, 1891, LIII. p. 160). Working with eggs of *Echinus*, Driesch found that if the first two segmentation-spheres were artificially separated, each grew into a separate *Pluteus*; if the separation was incomplete, the result was a double-monster, united by homologous surfaces. Similar experiments attended by similar results have since been made on *Amphioxus* by E. B. WILSON, *Anat. Anz.*, VII. 1892, p. 732.

[3] Evidence of such abrupt Variation between the two sides of the body belongs for the most part to the Substantive group.

possibility that the resemblance between the two sides of a bilaterally symmetrical body may be in some essentials the same as the resemblance between offspring of the same parent, or to use an inclusive expression, that the resemblance between the members of a Meristic Series may be essentially the same as the resemblance and relationship between the members of one family; that the members of a row of teeth in the jaw, of a row of peas in a pod, of a chain of Salps, or even a litter of pigs, all resulting alike from the processes of Division, may stand to each other in relationships which though different in degree may be the same in kind.

If reason shall appear hereafter for holding any such view as this, the result to the Study of Biology will be profound. For if it shall ever be possible to solve the problem of Symmetry, which may well be a mechanical one, we shall thus have laid a sure foundation from which to attack the higher problem of Variation, and the road through the mystery of Species may thus be found in the facts of Symmetry.

SECTION VIII.

DISCONTINUITY IN SUBSTANTIVE VARIATION: SIZE.

From the subject of Merism and the thoughts which it suggests, we now pass to another matter. The first limitation by which we proposed to group Variations was found in the characters which they affect: the second relates to the magnitude, or as I shall call it, the **Continuity** of the variations themselves. And though for many a conception has no value till it be cast in some finite mould, my aim will be rather to describe than to define the meaning of the term Continuity as applied to Variation. In dealing with a subject of this obscurity, where the outlines are doubtful, an exact mapping of the facts cannot be made and ought not to be attempted; but I trust that from the present indications, vague though they are, some larger and more definite conception of Discontinuity in Variation may shape itself hereafter by a process of natural growth. For this reason I shall as far as possible avail myself of examples rather than of general expressions, whether inclusive or exclusive.

To those who have studied the recent works of Galton, the conceptions here outlined will be familiar. In the chapter on "Organic Stability" in *Natural Inheritance*, the matter has been set forth with charming lucidity, and what follows will serve chiefly to illustrate the manner in which the facts of Natural History correspond with the suggestions there made.

In the case of most species it is a matter of common knowledge that though no two individuals are identical, there are many which in the aggregate of their characters nearly approach each other, constituting thus a normal, from which comparatively few differ widely. In such a species the magnitude of these differences is proportional to the rarity of their occurrence. Now this, which is a matter of common experience, has been shewn by Galton to be actually true of several quantities which in the case of Man are capable of arithmetical estimation. In the cases referred to it has thus been established that these quantities when marshalled in order give rise to a curve which is a normal curve of Frequency of Error. Taking for instance the case of stature, Galton's statistics shew that for a given community there is a mean stature, and the distribution of the statures of that community around the mean gives rise to a Curve of Error. In this case the individuals of that community in respect of stature form one group. Now in the case of a collection of individuals which can be separated into two species, there is some character in respect of which, when arranged by their statistical method, the individuals do not make one group but two groups, and the distribution of each group in respect of that character cannot be arranged in one Curve of Error, though it may give rise to two such curves, each having its respective mean. For example, if in a community tall individuals were common and short individuals were common, but persons of medium height were rare, the measurements of the Stature of such a community when arranged in the graphic method would not form one Curve of Error, though they might and probably would form two. There would thus be a normal for the tall breed, and a normal for the short breed. Such a community would, in respect of Stature, be what is called *dimorphic.* The other case, in which the whole community, grouped according to the degrees in which they display a given character, forms one Curve of Error, may conveniently be called *monomorphic* in respect of that character. By considering the possible ways in which such a condition of dimorphism may arise in a monomorphic community, one of the uses of the term Discontinuity as applied to Variation will be made clear.

Considering therefore some one character alone, in a species which is monomorphic in respect to that character, individuals possessing it in its mean form are common while the extremes are rare; while if the species is dimorphic the extremes are common and the mean is rare. Now the change from the monomorphic condition to the dimorphic may have been effected with various degrees of rapidity: for the frequency of the occurrence of the mean form may have gradually diminished, while that of the extremes gradually increased, through the agency of Natural Selection or otherwise, in a long series of generations; or on the other hand the diminution in the relative numbers of the mean individuals may have been rapid and have been brought about in a few generations by a few large and decisive changes, whether of environment or of organism.

Referring to the curve of Distribution formed in the graphic method of displaying the statistics, during the monomorphic period the curve has one apex corresponding with the greatest frequency of one normal form, but in the dimorphic period the curve has two apices, corresponding with the comparative frequency of the two extremes, and the comparative rarity of the mean form. The terms Continuous or Discontinuous are applicable to the process of transition from the monomorphic to the dimorphic state according as the steps by which this change was effected are small or large.

The further meanings of Discontinuous Variation will be explained by the help of examples. The first cases refer to Substantive Variation[1], and we may conveniently begin by examining a case of Variation in a character which is easily measured arithmetically.

Among beetles belonging to the Lamellicorn family there are numerous genera in which the males may have long horns arising from various parts of the head and thorax[2]. These horns may be

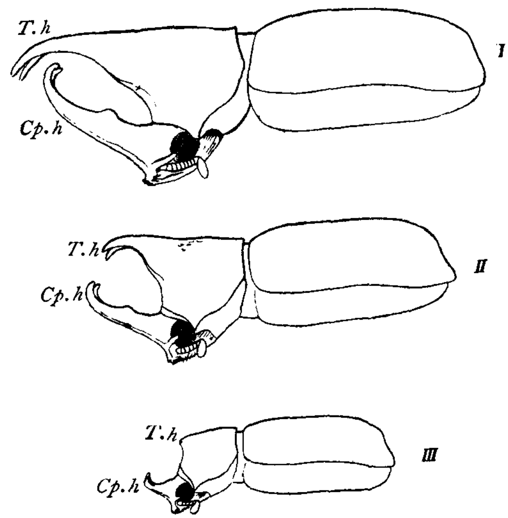

FIG. 1. Side-views of the Lamellicorn beetle, *Xylotrupes gideon*. Legs not represented. I, High male, II, Medium male, III, Low male.

[1] In referring thus to evidence as to Substantive Variation, I find myself in the difficulty mentioned in the Preface. For it is necessary to allude to matters which cannot be properly treated in this first instalment of facts. In order, however, that the one introductory account may serve for all the evidence together, such allusion is inevitable and I can only trust that full evidence as to Substantive Variation may be produced before long.

[2] For particulars of this subject with illustrations, see *Descent of Man*, 1st ed., vol. I. pp. 369—372. A detailed account of this and the succeeding example in the case of the Earwig was given by Mr Brindley and myself in *P. Z. S.*, 1893.

of very great size, as in the well-known Hercules beetle (*Dynastes hercules*) and others. The females of these forms are usually without horns. In such genera it is commonly found that the males are not all alike, but some are of about the size of the females and have little or no development of horns, while others are more than twice the size of the females and have enormous horns. These two forms of male are called "low" and "high" males respectively.

In many places in the Tropics such beetles abound, both "high" and "low" males occurring in the same locality. An admirable example of this phenomenon is seen in *Xylotrupes gideon*, of which a "high," "low," and medium male are shewn in profile in Fig. 1. Of this insect a very large number were kindly given to me by Baron Anatole von Hügel, who collected them at one time, in one locality, in Java. In this species there is one cephalic and one thoracic horn, placed in the positions shewn in the figure. Fig. 1, I shews a "high" male, II is a medium, and III a "low" male. In the gathering received there were 342 males. My friend, Mr H. H. Brindley, has made careful measurements of the lengths of the horns of these specimens and has constructed the diagram, Fig. 2. In this each dot represents an individual, and the abscissæ shew the measurements of the length of the cephalic horn. For clearness these measurements are represented as of twice the natural size. So far as the numbers go the result shews that the most frequent forms are

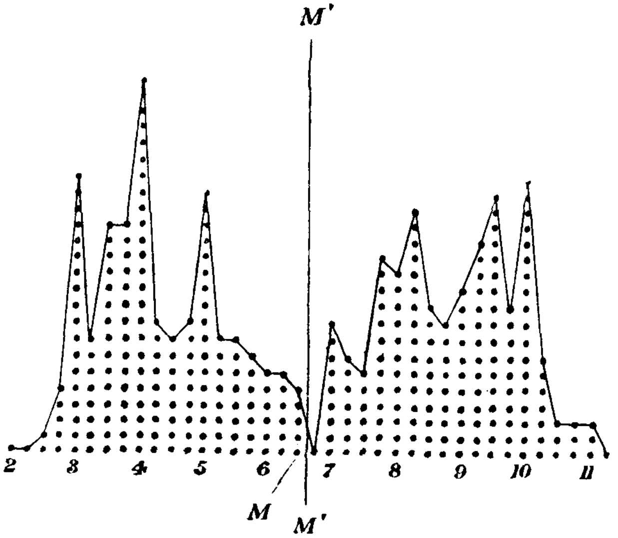

FIG. 2. Diagram representing the frequency of the lengths of cephalic horn in male *Xylotrupes gideon*. M, the mean case; *M'* the mean value. The abscissæ give lengths of cephalic horn in lines.

the moderately low and the moderately high, the forms of mean measurement being comparatively scarce. It is true that the numbers are few, but so little heed is paid to phenomena of this kind that material is difficult to obtain and the present opportunity was indeed wholly exceptional[1]. But taking the evidence for what it is worth, the comparative scarcity of "medium" males in that particular sample is clear, and so far the form is dimorphic, and has two male normals.

Now such a condition may have arisen in several ways. First, in the past history of the species there may have been a time when the males were horned and were monomorphic, the "medium" form being the most frequent, and the present dimorphic condition may have been derived from this, either continuously or discontinuously as described above for the case of Stature. Secondly, the dimorphism may date from the first acquisition of the horns, and this character may perhaps have always been distributed in the dimorphic way. In this case the term Discontinuous would be applicable to the Variation by which the groups of "high" and "low" males have been severally produced. I am not acquainted with evidence as to the course of inheritance in these cases, and I do not know therefore whether both "high" and "low" males may be produced by one mother. If this should be shewn to be the case, it would suggest that the separation of the males into two groups was a case of characters which do not readily blend, and are thus exempt from what Galton has called the Law of Regression[2].

In the case of a somewhat similar structure found in the Common Earwig (*Forficula auricularia*) the dimorphism is still more definite. In the autumn of 1892 on a visit to the Farne Islands, a basaltic group off the coast of Northumberland, it was found that these islands teem with vast quantities of earwigs. The abundance of earwigs was extraordinary. They lay in almost continuous sheets under every stone and tussock, both among the sea-birds' nests and by the light-keepers' cottages. Among them were males of the two kinds shewn in Fig. 3; the one or high male having forceps of unusual length, the other or low male, being the common form. It appears that the high male is known from many places in England and elsewhere and that it was made into a distinct species, *F. forcipata*, by

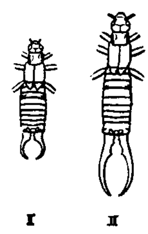

FIG. 3. I, High male, II, Low male of Common Earwig (*Forficula auricularia*) from the Farne Islands.

[1] In the Lucanidæ, of which the Stagbeetle (*L. cervus*) is an example, a similar phenomenon occurs, the "high" and "low" males being distinguished by the degree of development of the mandibles. No sufficient number of male Stagbeetles has yet been received to warrant any statement as to the frequency of the various types of males.

[2] *Natural Inheritance*, pp. 88—110.

STEVENS[1] though by later authorities[2] the species has not been retained. A large sample of Earwigs collected in a Cambridge garden contained 163 males of which 5 would come into the high class, but the great abundance of high males at the Farnes seems to be quite exceptional.

With a view to a statistical determination of the frequency of the high and low forms 1000 of these Earwigs were collected by Miss A. Bateson, the whole being taken at random on one day from three very small islands joined to each other at low tide. Of the 1000 specimens 583 proved to be mature males with elytra fully developed, no specimen with imperfect elytra being included in this number[3]. On measuring the length of the forceps to the nearest half mm. and grouping the results in the graphic method the curve shewn in Fig. 4 was produced. The figures on the

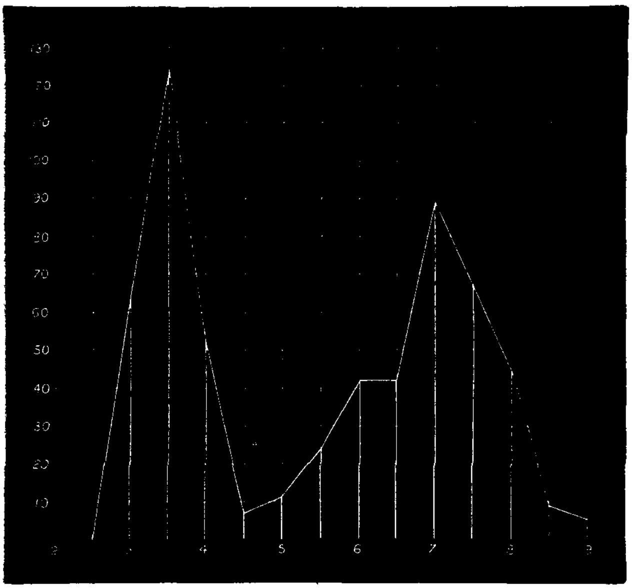

FIG. 4. Curve shewing frequency of various lengths of forceps of male Earwigs (*F. auricularia*) from the Farne Islands. Ordinates, numbers of individuals: abscissæ, lengths of forceps in mm.

ordinates here shew the numbers of individuals, those on the abscissæ giving the length of the forceps in millimetres. As there

[1] STEVENS, *Brit. Ent.* 1835, VI. p. 6, Pl. XXVIII. fig. 4.

[2] FISCHER, *Orthop. Europ.*, 1853, p. 74; BRUNNER VON WATTENWYL, *Prodr. d. europ. Orthop.*, 1882, p. 12.

[3] For particulars in evidence of the maturity of these specimens see *P. Z. S.*, 1893.

shewn the smallest length of forceps was 2·5 mm., and the greatest 9 mm., the greatest frequency being grouped about 3·5 mm. and 7 mm. respectively. The mean form having forceps of moderate length is comparatively rare. The size of the forceps of the females scarcely varies at all, probably less than 1 mm. in the whole sample.

The number of cases is enough to fairly justify the acceptance of these statistics and it is not likely that a greater number of cases would much alter the shape of the curve. Here, therefore, is a group of individuals living in close communion with each other, high and low, under the same stones. No external circumstance can be seen to divide them, yet they are found to consist of two well-marked groups.

Before leaving these examples special attention should be directed to the fact that the existence of a complete series of individuals, having every shade of development between the "lowest" and the "highest" male, does not in any way touch the fact that the Variation may be Discontinuous; for we are concerned not with the question whether or no all intermediate gradations are possible or have ever existed, but with the wholly different question whether or no the normal form has passed through each of these intermediate conditions. To employ the metaphor which Galton has used so well—and which may prove hereafter to be more than a metaphor—we are concerned with the question of the positions of Organic Stability; and in so far as the intermediate forms are not or have not been positions of Organic Stability, in so far is the Variation discontinuous. Supposing, then, that the "high" and "low" males should become segregated into two species—a highly improbable contingency—these two species would have arisen by Variation which is continuous or discontinuous according to the answer which this question may receive.

SECTION IX.

DISCONTINUITY IN SUBSTANTIVE VARIATION: COLOUR AND COLOUR-PATTERNS.

From the consideration of Discontinuity in the Variation of a character, size, which may be readily measured arithmetically, we pass to the more complex subject of Discontinuous Variation in qualities which are not at once capable of quantitative estimation. In this connexion the case of colour-variation may be profitably considered. Nature abounds with examples of colour-polymorphism, and in numerous instances such Variation is discontinuous. Of such discontinuous Variation in colour I shall speak under two heads, considering first variations in colours themselves and secondly variations in colour-patterns. As it is not proposed to give the evidence as to Substantive Variation in this volume, a few examples must suffice to shew the use of the term Discontinuity as applied to these Colour-variations.

I. *Colours.* The case of the eye-colour of Man may well be mentioned first, as it has been studied statistically by Galton. In this case the facts clearly shewed that certain types of eye-colour are relatively common and that intermediates between these types are comparatively rare. The statistics further shewed that in this respect inheritance was alternative, and that the different types of eye-colour do not often blend in the offspring. "If one parent has a light eye-colour and the other a dark eye-colour, some of the children will, as a rule, be light and the rest dark; they will seldom be medium eye-coloured, like the children of medium eye-coloured parents.[1]"

Colour dimorphism of this kind is very common among animals and plants. It is well known, for example, among beetles. Several metallic blue beetles have bronze varieties of both sexes, living together in the same locality. A familiar instance of this dimorphism occurs in the common *Phratora vitellinæ.* Again in the Elaterid beetle, *Corymbites cupreus,* there is a similar dimorphism in both sexes, the one variety having elytra in larger part yellow-brown, while the elytra of the other are metallic blue. This blue variety was formerly reckoned a distinct species, *C. æruginosus.* In the latter case I am informed by Dr Sharp, who has had a large experience of this species, that no intermediate between these two varieties has been recorded, and in the case of the *Phratora* the occurrence of intermediates is very doubtful. Another common example of colour dimorphism is seen in *Telephorus lividus,* the "sailor" of "soldiers and sailors." This beetle may be found in large numbers, about half being slaty in colour (var. *dispar*), while the remainder have the yellowish colour which coleopterists call "testaceous." Such instances may be multiplied indefinitely. When the whole evidence is examined it will be found that different colours are liable to different discontinuous variations; as instances may be mentioned black and tan in dogs; olive-brown or green and yellow in birds, &c.[2]; grey and cream-

[1] *Natural Inheritance,* p. 139.

[2] A specimen of the green Ring Parakeet (*Palæornis torquatus*) at the Zoological Society's Gardens was almost entirely canary-yellow in 1890. Since that date it has become more and more "ticked" with green feathers. A Green Woodpecker (*Picus viridis*) is described, having the feathers of the rump edged with red instead of yellow, the normally green feathers of the three lower rows of wing-covers and the back were pointed with yellow. J. H. GURNEY, *Zoologist,* XI. p. 3800. I am indebted to Mr Gurney for the loan of a coloured drawing of this specimen. Another example is described as being entirely canary-yellow, with the exception of a few feathers on the cap, which were purple-red. DE BETTA, *Mater. per una fauna Veronese,* p. 174. For this reference I am indebted to Prof. Newton. Specimen of Common Bunting whitish yellow. EDWARD, *Zool.,* 6492; Sedge Warbler canary-yellow. BIRD, *Zool.,* 3632. The Canary itself is a similar case. An Eel gamboge-yellow. GURNEY, *Zool.,* 3599.

colour in mice and cygnets[1]; red and blue in the eggs of many Copepoda[2], the tibiæ of Locusts[3], the hind wings of the Crimson Underwing (*Catocala nupta*)[4], &c. Another case of blue as a variety of scarlet is the familiar one of the flower of the Pimpernel (*Anagallis arvensis*). Discontinuous colour-variation of this kind is one of the commonest phenomena in nature, but to advance the subject materially it is necessary for a large mass of evidence to be produced. This cannot now be attempted, but in order to bring out the close relation between these facts and the problem of Species I propose to dwell rather longer on one special section of the evidence which must serve to exemplify the rest. The case which I propose to take is that of certain yellow, orange, and red pigments. For brevity I shall present the chief facts in the first instance without comment.

1. *Colias edusa* (Clouded Yellow) is usually orange-yellow, having a definite pale yellow female variety, *helice*, which is not recognized as occurring in the male form. A specimen is figured having the right side *helice* and the left *edusa*. FITCH, E. A., *Entomologist*, 1878, XLI. p. 52, Pl. fig. 11. This was an authentic specimen, for Mr Fitch tells me that it was taken by his son and seen alive by himself.

A specimen having one wing white and the rest orange is recorded by MORRIS, *Brit. But.*, p. 13.

Intermediates between *edusa* and *helice* must be exceedingly rare. OBERTHÜR records two such specimens and says that STAUDINGER took a similar one at Cadiz. For this intermediate he proposes a new name, *helicina*. *Bull. Soc. Ent. Fr.* (5), x. p. cxlv.

[1] In this case I can affirm the alternative character of the inheritance. For several years a pair of swans kept by St John's College, Cambridge, have produced cygnets, some of which have been of the normal grey, while others have been fawn-colour, a condition which Prof. Newton tells me has been thought characteristic of the "Polish" swan, a putative species. None of these cygnets are intermediate in colour, and all acquire the full white adult plumage, but the feet of the fawn-coloured cygnets remain pale in colour. Now the father of these has pale feet and was doubtless himself a fawn-coloured cygnet; the hen is normal. The cock formerly belonged to Dr Gifford, who kindly told me that the cygnets of this bird by a different hen were also thus diverse. A pair of these were given to Sir John Gibbons, who informs me that "from these there has been a brood every year, and always I think *one* of the cygnets has been white or nearly so, the others being of the usual colour." One of Dr Gifford's birds was also given to the late Mrs Gosselin of Blakesware, to whom I am indebted for descriptions of and feathers from several fawn-coloured cygnets which were its offspring. A similar case on the Lake of Geneva is recorded by FAUVEL, *Rev. Zool.*, 1869, p. 334, and another in the Zool. Gardens at Amsterdam, by NEWTON, *Zool. Rec.*, 1869, p. 99.

[2] This is well known to collectors of fresh-water fauna, and I have repeatedly seen the same phenomenon in species of *Diaptomus*, especially *D. asiaticus*, in the lakes of W. Siberia. Among thousands of individuals with red-brown egg-sacs, will often occur a few specimens having the egg-sacs of a brilliant turquoise-blue. In this connexion compare the case of the Crayfish (*Astacus fluviatilis*), which turns scarlet on being boiled, and which, like the Lobster, not uncommonly appears in a full blue variety.

[3] *Caloptenus spretus* with hind tibiæ blue instead of red, DODGE, *Can. Ent.*, 1878, x. p. 105; *Melanoplus packardii*, having hind tibiæ red instead of bluish, BRUNER, *Can. Ent.*, 1885, XVII. p. 18. For reference to these observations I am indebted to COCKERELL, *Ent.*, 1889, XXII. p. 127.

[4] WHITE, *Ent.*, 1889, XXII. p. 51. Compare the fact that in another species of *Catocala* (*C. fraxini*), the Clifden Nonpareil, the hind wings are normally bluish.

A curious specimen, apparently a *male*, having the colour of *helice* was kindly shewn me by Mr F. H. WATERHOUSE. The light marks which in the female are present on the dark borders of the fore-wing are only represented by one minute light mark on each fore-wing.

In most if not all of the *edusa* group of *Colias*, there is a pale aberration of the female, corresponding to the *helice* variety of *edusa*. ELWES, *Tr. Ent. Soc.*, 1880, p. 134. In the same paper is a full account of the geographical distribution of the several species and colour-varieties of *Colias*.

Colias hyale (Pale Clouded Yellow) is normally sulphur-coloured. Nearly white varieties and a variety with the field rich sulphur colour, and the apical marginal patches red, are recorded in several works.

2. *Gonepteryx rhamni* (The Brimstone) is sulphur-yellow in the male, and greenish-white in the female. There is a spot in each wing, and the scales covering this on the upper side are bright orange.

Gonepteryx cleopatra, a S. European species, is like the above in the hind-wings, while the field of the fore-wings is flushed with orange of exactly the tint of that on the spots of *G. rhamni*.

There are several records in entomological literature alleging the capture of "*G. cleopatra*" in Britain, e.g. *Proc. Ent. Soc.*, 1887, p. xliii.

In addition to these there are records of specimens of *G. rhamni* more or less flushed with orange; e.g., a specimen at Aldershot with orange spots on fore-wings as in *cleopatra*, *Proc. Ent. Soc.*, 1885, p. xxiv. Mr Jenner Weir said he had seen a specimen in Ingall's collection, intermediate between *rhamni* and *cleopatra*. *ibid.*

A male of *G. rhamni* taken at Beckenham had the costal margin of each fore-wing broadly but unequally suffused with bright rose-colour or scarlet, and the right posterior wing was marked in like manner. The insect was thus marked when captured. BICKNELL, *Proc. Ent. Soc.*, 1871, p. xviii.

3. *Anthocharis* (*Euchloe*) *cardamines* (The Orange Tip), in the male has the fore-wings tipped with orange on both sides, while in the female these orange tips are absent. The field in both is white. In entomological literature are many records of variations in the extent and depth of the orange markings on upper or under side, or both (cp. *Zoologist*, xiii. 4562; *Proc. Ent. Soc.*, 1870, p. ii.; MOSLEY, *Illustrations of British Lepidoptera*; HAWORTH; BOISDUVAL and many others), but with these we are not immediately concerned.

A specimen is figured in which the orange spots were completely represented by yellow. MOSLEY, *Illustrated Brit. Lep.*

The white of the field is replaced by primrose or lemon yellow in several Continental forms. These have been described as species under the names *eupheno*, *belia*, *euphenoides*, *gruneri*, &c.

A local variety of *A. eupheno* is described from Mogador, where it was found common at a little distance from the town. The female was much larger than the type, resembling the male in markings and in shape of the fore-wings. The orange blotch, instead of being confined to tip of the fore-wing as normally, extends to the discoidal spot and is usually bounded by a black band, sometimes suffusing the whole tip of the wing. The colour of the field varies from pure white to pale lemon: the hind-wings are always yellower than in the type, in some specimens being nearly as yellow as those of the male. Mr M. C. Oberthür supplied a specimen from Central Algeria which was intermediate between the type and this variety. LEECH, J. H., *P. Z. S.*, 1886, p. 122.

4. Amongst Lepidoptera the change from red to yellow is very common. A case of *Vanessa atalanta*, having the red partially replaced by yellow, is figured in *Entom.*, 1878, XI. p. 170, *Plate.* Varieties of *Arctia caja*, *Callimorpha dominula*, *C. hebe*, *C. hera*, *C. jacoboeæ*, *Zygæna filipendulæ*, *Z. minos*, &c., with yellow instead of red, are to be seen in many collections. See especially OCHSENHEIMER, *Schm. v. Europa*, 1808, II. p. x, also p. 25, and many other authors. A chalk-pit at Madingley, Cambridge, has long been known to collectors as a locality for the yellow *Z. filipendulæ* (Six-spot-Burnet); see *Ent. Mo. Mag.* XXV. p. 289. In some of these the yellow is tinged with red, but it is commonly a very distinct variety. A variety of the Red Underwing (*Catocala nupta*) with brownish-yellow in the place of the red, is figured by ENGRAMELLE, *Papill. d'Eur.*, Pl. CCCXXII. The evidence relating to this subject is very extensive, and concerns many genera and species besides those named above.

5. *Pericrocotus flammeus* (an Indian Fly-catcher) is grey and yellow in the female, and black and orange-red in the male. The young male is grey and yellow like the female. An adult male is described in which the grey had been fully replaced by black, but the yellow remained, not having been replaced by red. R. G. WARDLAW RAMSAY, *P. Z. S.*, 1879, p. 765. See also LEGGE, *Birds of Ceylon*, I. p. 363, for description of male in transitional plumage.

Curiously enough the change from red to yellow and from light yellow to dark is no less common among plants, though it can scarcely be supposed that the substances concerned are similar.

1. *Narcissus corbularia* and other species are known in sulphur-yellow and in full yellow[1].

2. The Iceland Poppy (*P. nudicaule*) is very common in gardens under three forms, white, yellow and orange. Intermediate and flaked varieties occur, but are less common than the three chief forms. Respecting this species Miss Jekyll of Munstead, who first brought out the varieties, kindly gives me the following information. She writes:—"I began with one plant of the yellow colour that I take to be the type-colour. It was then new as a garden plant, so I saved the seed. The first sowing gave me various shades of orange, as well as the type, in different shades. In the 3rd and 4th years I got buffs, whites, and very pale lemon colourings. As there was only one plant to begin with there was no question of cross-fertilization. A white appeared in the 3rd year of sowing and I kept on selecting for 2 or 3 years......and gave it to a friend in Ireland, who returned it to me 2 years later still more improved. This strong white seems now to be fixed and quite unwilling to revert to the yellow colourings, and is a rather stouter and

[1] Mr P. Barr, who has collected these forms in Portugal, tells me that he believes the pale ("*citrina*") varieties of *N. ajax* and *N. corbularia* to be confined to calcareous soils.

handsomer plant altogether." In seedlings from the orange or yellow form grown in separate beds the proportion of seedlings true to their parent colour would not be nearer than about 60 or 70 per cent., but in the case of the white form Miss Jekyll considers that 95 per cent. may be expected to come true.

The yellow Horned Poppy (*Glaucium luteum*) is normally of a lemon yellow very like that of *P. nudicaule*. Of this species also there is an orange cultivated variety. The varieties of the tomato offer a similar series of colour-variations.

3. Fruits of many kinds are known in red and yellow forms. For instance the yellow berried Yew is well known. It is described under the name *Taxus baccata fructu-luteo*, LOUD. "It appears to have been discovered about *1817* by Mr *Whitlaw of Dublin, growing* in the demesne of the Bishop of Kildare, near Glasnevin; but it appears to have been neglected till 1833 when Miss Blackwood discovered a tree of it in Clontarf churchyard near Dublin. Mr Mackay on looking for this tree in 1837 found no tree in the churchyard, but several in the grounds of Clontarf Castle, and one, a large one, with its branches overhanging the churchyard, from which he sent us specimens. The tree does not differ, either in its shape or foliage, from the common yew, but when covered with its berries it forms a very beautiful object, especially when contrasted with yew trees covered with berries of the usual coral colour." LOUDON, *Arb. et Frut. Brit.*, IV. 1838, p. 2068.

4. The Raspberry (*Rubus idæus*) is another fruit which is known wild in both the red and yellow forms, though the latter is less common. According to BABINGTON, it has pale prickles, and leaflets rather obovate. *Brit. Rubi*, p. 43. (See RIVERS, *Gard. Chron.*, 1867, p. 516.)

Any person who has opportunities of handling animals and plants in numbers can add many similar cases. These few are taken more or less at random, as illustrations of the frequency with which red, orange, and yellow may vary to each other. It is of course not necessary to say that in numerous instances both among animals and plants, the same parts which in one species are yellow, in an allied species or in a geographically distinct race are represented by orange or by red. To an appreciation of the rapidity with which such changes may have come about, facts like the foregoing contribute.

The frequency of such variations suggest that many of these yellow and red pigments are either closely allied bodies or different forms of the same body. Until the chemistry of these substances has been properly investigated nothing can be definitely stated as to this, but the fact that vegetable yellows are very sensitive to reagents is familiar. The lemon variety of the Iceland Poppy treated with ammonia turns to a colour almost identical with that of the orange variety, while the white variety so treated goes primrose yellow. The lemon variety when boiled, or treated with alcohol yields an orange solution, which is of the same tint. This returns to lemon-colour if treated with ammonia or acids. The wings of *G. rhamni* when boiled yield a soluble yellow, which according to HOPKINS (*Proc. Chem. Soc.*, reported *Nature*, Dec. 31, 1891) is a derivative of mycomelic acid, allied to uric acid. This substance turns orange with reagents. The wings of *G. rhamni* turn orange-red when exposed to wet potassium cyanide (*Proc. Ent. Soc.*, 1871, p. xviii) as may be easily seen.

When these facts, meagre though they are, are considered together with the evidence of variability, the suggestion is very strong that the discontinuity between these several characteristic colours is of a chemical nature, and that the transitions from one shade of yellow to another, or from yellow to orange or red is a phenomenon comparable with the changes of litmus and some other vegetable blues from blue to red or of turmeric from yellow to brown. If such a view of these phenomena were to be accepted, it would, I think, be simpler to regard the constancy of the tints of the several species and the rarity of the intermediate varieties as a direct manifestation of the chemical stability or instability of the colouring matters, rather than as the consequences of environmental Selection for some special fitness as to whose nature we can make no guess. For we do know the phenomenon of chemical discontinuity, whatever may be its ultimate causes, but of these hypothetical fitnesses we know nothing, not even whether they exist or no.

II. *Colour-patterns.* Thus far I have spoken only of discontinuous variations in colours themselves, but there are no less remarkable instances of discontinuous variations in the distribution of colours in particoloured forms. By a combination of these modes, variations of great magnitude may occur.

One of the most obvious cases of this phenomenon is that of the Cat. In European towns cats are of many colours, but they nevertheless fall very readily into certain classes. The chief of these are black, tabby, silver-grey and silver-brindled, sandy, tortoiseshell, black and white, and white. Of course no two cats have identical colouring, but the individual variations group very easily round these centres, and intermediate forms which cannot at once be referred to any of these groups are immediately recognized as something out of the common and strange. Yet it is almost certain that cats of all shades breed freely together, and there is no reason to suppose that the discontinuity between the colour-groups is in any way determined by Natural Selection.

Another example may be seen in the Dog-whelk (*Purpura lapillus*). This animal occurs on nearly the whole British coast, wherever there are rocks or even clay hard enough to form definite crevices. Like most littoral animals, the Dog-whelks of each locality differ more or less from those of other localities, and these differences may be differences of size, texture of shell, degree of calcification, amount of "frilling," &c. The peculiarities may be so striking that each individual can at once be recognized as belonging to a given locality, or they may be trifling, and appreciable only when a large number of individuals are gathered. But apart from these differences of form and texture there are a great number of colour-varieties of which the following are the three chief whole-coloured forms, viz. white, dark purple-brown, and yellow. In addition to these there are banded forms, and the bands may be coloured with any two of the three colours mentioned above. Among the banded forms there are two distinct sorts of banding, in the one there are very many fine bands and in the other there are a few broad bands. In most localities these colour-varieties may all be found; though in some places, especially where the water is foul, as at Plymouth, the shells are greatly corroded and the colours, if originally present, are obscured. Speaking however of localities in which colour-varieties are to be seen at all, several may generally be found together. If any one will take the trouble to gather a few hundreds of these shells and will set himself to sort them into groups according to their colours, he will find that the majority fall naturally into groups of this kind; and that those which cannot be at once assigned to groups but fall intermediately between the groups are comparatively few. I have seen this at many places on the English coast; in Yorkshire, Norfolk, Suffolk, Kent, Sussex, Dorsetshire, Devonshire, Cornwall, &c. In several localities I have found pairs belonging to different colour-varieties breeding together, and there is therefore no reasonable doubt that these colour-variations do not freely blend, but are discontinuous.

The statements here made with regard to *P. lapillus* hold in almost the same way for *Littorina rudis*, but in this case the number of colour-types is larger. In *L. rudis* I have occasionally seen specimens of which the upper part belonged to one colour-type, and the lower to another, the transition occurring sharply at one of the varices. In these cases the shell appears to have been injured and is possibly renewed.

One of the commonest British Lady-birds (*Coccinella decempunctata*) is an extremely variable form. A great number of its varieties may be found together, ranging from forms with small black spots on a red field to forms in which the field is black with a few red spots. But in spite of the great diversity there are certain types which are again and again approached, while the intermediates are comparatively scarce.

The following case, well known to entomologists, may be mentioned here. The Painted Lady (*Pyrameis cardui*) is found in the typical form over the entire extent of every continent, with the exception of the Arctic regions and possibly S. America. A special form of it (var. *kershawi*) is found in Australia and New Zealand, but the other large islands south of Asia possess the normal type. The latter is also found in the Azores, Canaries, Madeira and St Helena. This butterfly has been taken on the snow-level in the Alps; and in N. America, though it may be regarded as one of the commonest butterflies in the elevated central district, it is most abundant at a level of 7000—8000 feet. It has been taken on Arapahoe Peak, between 11,000 and 12,000 feet (from Scudder, *Butterflies of N. America*, I. pp. 477—480). Of this insect, which is a very constant one, a certain striking aberration has been found, always as a great rarity, in many lands. In this aberration the markings are almost entirely rearranged. It is said to have been first described by Rambur under the name var. *Elymi*, but this description I have never found. (The reference quoted is *Annales des Sci. d'observation*, Paris, 1829, Vol. II. *Pl.* V.) As often happens with Variation, without coloured figures description is almost useless, but the figures referred to are very accessible. In a British specimen of this aberration the white bars are absent from the anterior costæ and a series of white fusiform blotches are present along the marginal border; two abnormal white spots are also present near the anal angle, thus continuing the series down the wing (*fig.* 5, A.). The hind-wings are equally aberrant. The two large dark spots which are usually on the disk between the median nervure and the inner margin are altogether wanting. Between each of the nervures of the hind-wing is a white spot, whereas in the normal form there is no white spot at all on the hind-wings. These white spots on the hind-wings form a row parallel to the border of the wing and, as it

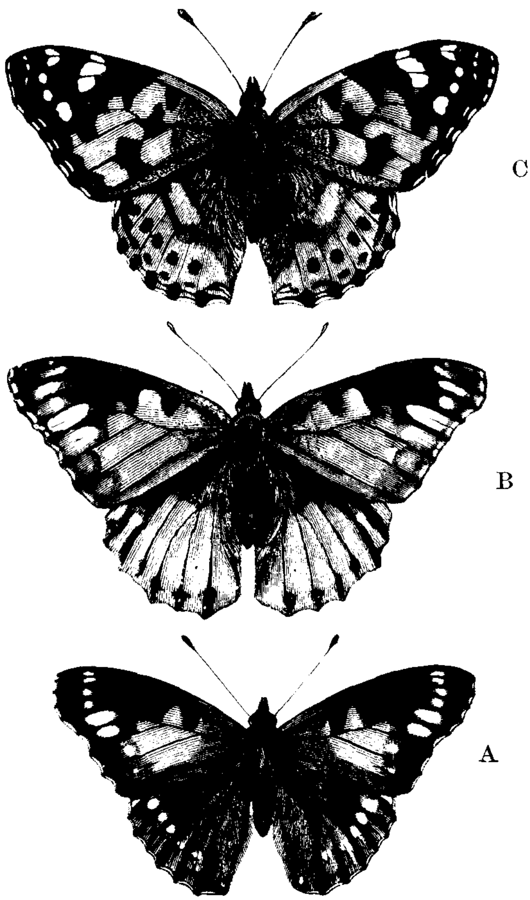

Fig. 5. A. Clark's specimen of *P. cardui*, var. *elymi* from *Ent.* 1880.
B. Newman's specimen. *Brit. But.*, p. 64.
C. *P. cardui*, normal, also from Newman. *Brit. But.*, p. 64.

were, continue the series of white spots borne by the anterior wings. [Underside *not described.*] *This specimen was reared from a larva found near the river Lea*, Clapton Park. CLARK, J. A., *Entomologist*, 1880, XIII. p. 73, *fig.* A coloured figure of the same specimen, MOSLEY, S. L., *Pl.* 8, *fig.* 3.

A form very closely similar to the above is figured in black and white by Newman from a specimen in Ingall's collection (*fig.* 5, B). [This is apparently the specimen given in *Zoologist*, p. 3304.] NEWMAN, *British Butterflies*, p. 64, *fig.* A British *specimen which nearly approaches this aberration in the absence of the* white bars *on the costæ and in the absence* of the black transverse bar is recorded. In it each of the sub-marginal rows of black spots on the posterior wings is drawn, containing a white spot. In this specimen the brown-red of the type was represented by rose-colour. NEWMAN, *Entomologist*, 1873, p. 345, *fig.*

Another specimen closely resembling this aberrant form is described from New South Wales. OLLIFF, A. S., *Proc. Linn. Soc.*, N. S. W., S. 2, III. p. 1250.

Another *specimen closely resembling* the above was taken at Graham's Town, S. Africa, and is mentioned by JENNER WEIR, *Entomologist*, 1889, XXII. p. 73.

Another specimen is figured in which the hind-wings are marked as in the above, but the anterior wings, though strongly resembling this aberration in the general disposition of the colours, yet differ in details, the chief points of difference being that the white costal bar is only partially obliterated and the white spots on *the anal angles of the fore-wings are not developed.*

[This specimen was in Kaden's collection and was presumably European.] HERRICH-SCHÄFFER, Bd. I. p. 41, *Pl.* 35, figs. 157 and 158.

A description is given of an aberrant form taken at King William's Town, S. Africa, which "closely resembled that figured by Herrich-Schäffer." TRIMEN, R., *South-African Butterflies*, I. p. 201.

A specimen (British) *resembling the above, but lacking the white spots on the* anal angles of the fore-wings and having the marginal row on the hind-wing light-coloured, but not quite white, is figured by MOSLEY, Pt. III. Pl. 3, *fig.* 3.

Two specimens were taken in New Jersey, U.S.A., which are stated to have conformed to this aberration. STRECKER, *Cat. N. Amer. Macrolepidop.*, p. 137.

Another British specimen generally resembling Herrich-Schäffer's figure is represented by MOSLEY, *Pl.* 8, fig. 4.

In all the above specimens the resemblance, as far at least as the upper surface is concerned, is considerable. With the exception of Herrich-Schäffer's example, the undersides are not figured, but from the descriptions it may be gathered that they also resembled each other though probably not so closely as the upper surfaces. The resemblance between the underside of the Australian specimen and that figured by Herrich-Schäffer must have been very close.

"Intermediate between these extreme sports and the normal form are three examples taken at Cape Town in 1866, 1873 and 1874—the first by myself—in which the fore-wing markings are scarcely affected, but the hind-wing spots are minutely ocellate and externally prolonged, so as to be confluent with the succeeding row of lunules." TRIMEN, *ibid.* pp. 201, 202.

Another aberration, a *Belgian specimen, resembles "Elymi" in kind but differs* from it in degree. In it also the white bars are absent from the costæ, and the brown and black markings of the anterior wings are rearranged in almost exactly the same manner. The posterior wings are modified to a much less extent and the normal row of black spots between the nervures remains, while only the first and second of the series of white spots is present, the former being very slight. In this individual *the markings of the underside also resemble the aberration generally*, but it retains the four ocelli of the type. DE DONCEEL, H. DONCKIER, *Ann. Soc. d'Ent. Belge*, 1878, XXI. p. 10, *Plate.*

A specimen, also Belgian, is described in which the two anterior wings resemble Herrich-Schäffer's figure in lacking the white bars on the costæ and in the arrangement of the black and ground colour. In neither of them are the white spots of the *anal angles (found in the British and Australian specimens) present.* The white markings at the apex of the anterior wings differ on the two sides, being in both of them unlike the type and an approach to the aberrations in question, but the degree to which they are developed differs markedly, being greatest on the right side. The *left* posterior wing resembles the aberration in having the six abnormal white spots, but less emphasized than in the figures quoted above; in general colour this wing is darker than the type. The *right* posterior wing, however, has none of the white spots of the aberration, and differs from the type only in being more suffused with black. To recapitulate, the two anterior and the left posterior wing resemble *generally*, though not entirely, the aberration, while the right posterior wing is nearly normal.

A specimen is described from Ekaterinoslav, S. Russia, which resembles this aberration in wanting the black transverse band and in the disposition of the apical white spots. A trace of the white costal bar remains on the costal border. On the underside of this specimen the ocelli were placed in a pale rose-coloured band. (Name proposed, aberration, *inornata*). BRAMSON, K. L., *Ann. Soc. Ent. France*, S. 6, VI. 1886, p. 284.

Besides the rare aberration "var. *Elymi*," there is a variety sometimes found in Europe, which in Australia is so constant and definite that it has been regarded as a species. The following may be quoted respecting its occurrence in Australia, where it is common:

"There is in abundance about Melbourne and in many other parts of Australia a *Cynthia* with the general appearance and habit of *C. cardui*, so closely represented that every entomologist I know refers it to that species. The Australian species differs from the European one constantly, however, in having the centres of the three lower round spots on the posterior wings bright blue, and having two other blue spots on the posterior angles of the same wings, the corresponding parts of the European form being black." For this form the name *C. kershawi* is proposed. M'COY, F., *Ann. and Mag. of Nat. Hist.*, Ser. 4, I. 1868, p. 76. See also OLLIFF, A. S., *Proc. Linn. Soc., N. S. W.*, Ser. 2, III. p. 1251. The notices of its occurrence in Europe are as follows. In 1884 Mr Jenner Weir exhibited a specimen of *P. cardui*, taken in the New Forest. Three of the five black spots in the disk of the upper side of the hind-wings had blue pupils; he pointed out that the specimen thus approached the Australian form, *P. kershawi*. *Proc. Ent. Soc.*, 1884, p. xxvii.

OLLIFF, *loc. cit.*, states that he has taken a specimen having these blue markings at Katwijk, in Holland.

In the case given, the evidence certainly suggests that these various forms of aberration are grouped round a normal form of aberration, just as the individuals of the type are grouped round its normal.

One example of a similar discontinuity in a melanic variation may profitably be given. I have taken this opportunity of referring to such a case, as the general evidence of melanic variations goes on the whole to shew that they are not commonly discontinuous, *and further evidence on this point would be most* valuable. To appreciate the evidence BUTLER'S coloured plate should be referred to.

Terias. A well-marked group of butterflies of this genus allied to *T. hecabe*, is found in Japan. It contains forms of great diversity in amount of black border which occurs on the outer margins of the fore- and hind-wings. The remainder of the wings is lemon-yellow. The black border may be confined to the tip of the fore-wings, or may there occupy a considerable area and be extended along the whole outer margin of both wings. The form with the least black is called *T. mandarina*, that with the most, is called *T. mariesii*, and the intermediate form is called *T. anemone*. Upwards of 150 specimens, all from Nikko, were examined; these ranged between the two extremes, and were found to form a continuous series. Butler states that "the absence of six of them, referable only to two gradations, would at once leave the three species as sharply defined as any in the genus."

[In the case of these butterflies, there are thus three groups of varieties, two extreme groups and one mean group; intermediates between these are comparatively rare. Butler suggests that these intermediate forms should be regarded as hybrids, even in the absence of experimental evidence. This view is of course dependent on the truth of the belief that such a discontinuous occurrence of variations is anomalous.]

Twenty specimens of the species *T. betheseba* and thirty-nine of *T. jaegeri* (both from Japan), were also examined. The former presented no variations whatever, and the latter only vary in the yellower or redder tint on the under surface of the secondaries. BUTLER, A. G., *Trans. Ent. Soc.*, 1880, p. 197, Pl. VI.

Compare the following:

Terias constantia. Twenty-five pupæ, all found together on the same twigs at Teapa, Tabasco, Mexico, by Mr H. H. Smith. The butterflies from these are in Messrs Godman and Salvin's collection, who kindly allowed me to examine them. The amount of black border on both wings varies much, nearly though not quite so much as in the cases figured by BUTLER. In the lightest the apex of the fore-wing alone is black, and there is no black on the hind-wing in 9 specimens; of the remaining 16 some have a well-defined black border to the hind-wing, while in the rest (about 6) this border is slight. This case is a particularly interesting one, as the specimens were associated and presumably belonged to one brood.

For another beautiful case of discontinuous Variation in pattern I am indebted to Dr D. Sharp. The Cambridge University Museum lately received a series of 38 specimens of *Kallima inachys,* the well-known butterfly whose folded wings resemble a dead leaf with its mid-rib and veinings. The underside of this butterfly is sometimes marked with large blotches and flecks of irregular shape, which, as has often been noted, resemble the patches of discoloration caused by fungi in decaying leaves. Dr Sharp pointed out to me that the specimens examined fell naturally into four groups according to the coloration of the underside. In the first group the field is nearly plain, though the tint varies in individuals. The "mid-rib" is strongly marked in this and all the groups, but the "veinings" are absent or very slightly marked in the first group: 18 specimens. In the second group the ground is almost plain, but it bears numerous strongly marked black-speckled spots, of forms which though irregular in outline are closely alike, and occupy the same positions in all the six specimens, being scarcely if at all represented in any of the others. In the third group the dark bars representing "veins" are strong, but the field is nearly uniform: 10 specimens. In the fourth group, of four specimens, the ground-colour is darkened in such a way as to leave large and definite blotches of light colour in particular places. Of these specimens three have the veinings very strongly marked, while the fourth is without them.

Into these four groups the specimens could be unhesitatingly separated, though in each group many individual differences occurred. No marked variation in the upper-sides was to be seen. These specimens were all from the Khasia hills, Assam, but there was of course no evidence that all were flying together.

One of the most interesting examples of discontinuous Variation in colour-patterns is the case of ocellar markings or eye-spots. Upon this subject nothing need here be said as the evidence will be given in detail in the course of this volume (see Chap. XIII.).

SECTION X.

DISCONTINUITY IN SUBSTANTIVE VARIATION.—MISCELLANEOUS EXAMPLES.

Of the discontinuous occurrence of Substantive Variation, the manifestations are many and diverse. We have seen that in such features as size, colour, and colour-patterns, Variations may be discontinuous, and a form may thus result, differing markedly from the type which begot it. Variation in the proportions or the constitution of essential parts may no less suddenly occur. The range of these phenomena is a large one, but for the purposes of this Introduction a few examples must suffice in general illustration of their scope.

A discontinuous variation which is familiar to all is that of "reversed" varieties, especially of Molluscs and Flat-fishes. Such varieties are formed as optical images of the body of the type. In both of the groups named, some species are normally right-handed, others being normally left-handed, while as individual variations reversed examples are found. In Molluscs this is not peculiar to Gasteropods with spiral shells, but may occur also both in Limacidæ (slugs)[1] and in Lamellibranchs[2]. Such variation is commonly discontinuous, and the two conditions are alternative. The fact that the reversed condition may become a character of an established race is familiar in the case of *Fusus antiquus*. This shell is found in abundance as a fossil of the Norwich Crag, such specimens being normally left-handed, though the same species at the present day is a right-handed one. Of the left-handed form a colony was discovered by MACANDREW on the rocks in Vigo Bay[3]. It was there associated with certain other shells proper to the Norwich Crag. This discovery seemed to Edward Forbes to be so remarkable that he looked on it as corroborative evidence of a special connexion between the fauna of Vigo Bay and the Crag fossils[3]. Jeffreys had the same variety from Sicily[4].

[1] For example, a sinistral *Arion*, BAUDON, *Jour. de Conch.*, XXXII. 1884, p. 320, and many others.

[2] Sinistral *Tellina*, FISCHER, P., *Jour. de Conch.*, XXVIII. 1880, p. 234. The same is recorded in several other genera.

[3] Seven specimens, *Ann. N. H.*, 1849, p. 507.

[4] *Brit. Conch.*, I. p. 326.

That they may the better serve to bring out the significance of Discontinuity in Variation to the general theory of Descent, it may be well to choose some examples with reference to characters which when seen in domestic animals are looked on as especially the result of Selection.

In exoskeletal structures several of this kind are known. From time to time there have been records of captures of the "hairy variety" of the Moorhen (*Gallinula chloropus*), in which the feathers were destitute of barbules and consequently had a hairy texture, greatly changing the general appearance of the bird.

Of the "hairy" variety twelve specimens were recorded, five from Norfolk, and the rest from Cambridgeshire, Hampshire, Sussex (2), Suffolk, Nottinghamshire and Athlone in Ireland. The tips of the barbs and shafts of the feathers have been broken off and the barbules are entirely wanting, giving a hairy appearance. This appearance was found in the whole of the plumage. Owing to the absence of barbules, the general coloration is tawny. A few feathers of this kind have been found in Hawks and Gulls, and in the case of a *Parra* (a bird which bears considerable resemblance to a Moorhen), lent to Mr Gurney by Professor Newton, a great portion of the body feathers were in this condition. The feathers of the *Apteryx* and Cassowary are also partially destitute of barbules. Mr Gurney was informed of a single case of a Grey Brahma hen which shewed the same peculiarity which appears otherwise to be without parallel. The case of the Silky Fowl is similar in the absence of most of the barbules, but in it the point of the shaft is produced to a delicate point, and the barbs are fine and sometimes bifid or trifid at the apex. From J. H. GURNEY, *Trans. Norwich Nat. Soc.*, III. p. 581, *Plate.* [Bibliography given.] [If another "hairy" Moorhen is found, note of the colour of the skin and bones should be made, for, as is well known, in the Silky Fowl they are purplish blue.]

The following may be compared: "Cochins are now and then met with in which the webs of the feathers having no adhesion, the whole plumage assumes a silky or flossy character like that of the Silky Fowl. It usually occurs quite accidentally, and in every case we have met with, the variety has been Buff. By careful breeding the character can be transmitted, but we have only known *one* case in which there had been this hereditary character, the others having been of accidental occurrence. Such birds are sometimes called 'Emu' fowls." LEWIS WRIGHT, *Illust. Book of Poultry*, 1886, p. 230.

Of many domestic animals, for example, the goat, cat and rabbit, varieties with long, silky hair are familiar under the name of "Angoras." Very similar breeds of guinea-pigs are kept, to which the name "Peruvian" is given. In this connexion the capture of a mouse (*Mus musculus*) with long, black, silk-like hair is interesting[1], as shewing that such a total variation may occur as a definite phenomenon without Selection.

[1] COCKS, W. P., *Trans. Cornwall Polytech. Soc.*, 1852. Like other animals, mice have of course often been found black. For instance, a number of black mice were found in Hampstead-down Wood. HEWETT, W., *Zool. Jour.* IV. p. 348.

As to the partial nakedness of the skin of many animals (Man, &c.), several suggestions have been made. It has been variously supposed that the covering of hair has been gradually lost by Man, in correlation with the use of clothes; with the heat of the sun; for ornamental purposes under sexual selection[1]; or perhaps as a protection from parasites[2]. Various suggestions have also been made to explain the persistence of hair at the junction of the limbs and on the head and face. To a consideration of the origin of nakedness, the evidence of Variation in some measure contributes, and though the bearing is not very direct, it may illustrate the futility of inquiries of this kind made without regard to the facts of Variation.

MOUSE (*Mus musculus*): male and pregnant female found in a straw-rick at Taplow; both were entirely naked, being without hairs at all, excepting only a few dark-coloured whiskers. The skin was thrown up into numerous prominent folds, transversely traversing the body in an undulating manner. This condition of the skin obtained for them the name of "Rhinoceros mice." The ears were dark or blackish, the tail ash-coloured, and the eyes black, indicating that they were not albinos. The exfoliations from the skin were examined microscopically but no trace of hair-follicles was found, nor any suggestion of disease. The animals were active and healthy.

The young ones, when born, were similar to the parents. The teeth were normal.

In the Museum of the College of Surgeons is a precisely similar specimen which was found in a house in London. GASKOIN, *Proc. Zool. Soc.*, 1856, p. 38, *Plate.*

Three specimens of the common Mouse (*Mus musculus*) were caught in the town of Elgin. The whole bodies of these three creatures "were completely naked—as destitute of hair and as fair and smooth as a child's cheek. There was nothing peculiar about the snout, whiskers, ears, lower half of the legs and tail, all of which had hair of the usual length and colour. They had eyes as bright and dark as in the common variety......At least two others were killed in the same house where these were found." GORDON, G., *Zoologist*, 1850, VIII. p. 2763.

SHREW. (*Sorex* sp.) "whole of upper surface of head and body destitute of hair, and skin corrugated like that of Naked Mice figured in *P. Z. S.*, 1856;" sent to Brit. Mus. by Mr P. Garner. GRAY, J. E., *Ann. and Mag. of N. H.*, 1869, S. 4, IV. p. 360.

In connexion with these cases, the following fact is interesting:

Heterocephalus is a genus of burrowing rodent from S. Africa. It contains two species, of which one is about the size of a mouse and the other is rather larger. They are characterized by possessing an apparently hairless skin which is on the head and body of a wrinkled and warty nature. On closer inspection the skin is seen to be furnished with fine scattered hairs, but there is no general appearance of a hairy covering. There is no external ear in these animals. OLDFIELD THOMAS, *P. Z. S.*, 1885, p. 845, *Plate LIV.*

Naked horses have often been exhibited. Such a horse caught in a

[1] C. DARWIN, *Descent of Man*, I. p. 142.

[2] BELT, *Naturalist in Nicaragua;* see also HUDSON, *Naturalist in La Plata*, 1892.

semi-feral herd in Queensland was described by TEGETMEIER, *Field*, XLVIII. 1876, p. 281. The skin was black and like india-rubber. Careful examination shewed no trace of hair, or any opening of a hair-follicle. In Turkestan, in the year 1886, I heard of one thus travelling, but failed to see it. 'Hairless' dogs in S. America remain distinct (BELT, *l. c.*).

Of discontinuous Substantive Variation in bodily proportions a single example must suffice. Among domestic animals of many kinds, races are known in which the bones of the face do not grow to their full size, while the bones of the jaw are, or may be, of normal proportions. Familiar examples of this are the bull-dog, the pug, the Japanese pug, the Niata cattle of La Plata[1], some short-faced breeds of pigs, and others. In the case of these domestic animals the part which Selection has taken in their production is unknown, and the magnitude of the original variations cannot be ascertained. It is nevertheless of interest to notice that parallel variations have occurred in distinct forms, and I think that this is to some extent evidence that the variations were from the first definite and striking. As regards the dogs even, there is a presumption that the short face of at least the Japanese pug arose independently from that of the common, or Dutch pug (as it used to be called), but as to this the evidence is insufficient. Among the dogs' skulls found in ancient Inca interments, a skull was found having the form of the bull-dog. NEHRING, *Kosmos*, 1884, XV. As these remains belong to a period before the European invasion, it is most probable that this bull-dog breed arose independently of ours.

Apart however from domestic animals there is evidence as to the origin of short-faced breeds. This evidence, which is not so well-known as it deserves to be, is provided by the occurrence of a similar variation in fishes. Darwin in speaking of the evidence as to Niata cattle makes allusion to the case of fishes in a note[2], quoting WYMAN as to the cod, which occurs in a form known to fishermen as the "bull-dog" cod. The interest of this observation is increased by the fact that it does not stand alone, but similar variations have been seen in the carp, chub, minnow, pike, mullet, salmon and trout. In the last-named there is even evidence of the establishment of a local race having this singular character.

CARP (*Cyprinus carpio*). "Bull-dog"-headed Carp have often been described. The face ends more or less abruptly in front of the eyes, while the lower jaw has almost its normal length. The front part of the head is bulging and prominent, giving the fish an appearance which several authors compare to that of a monumental dolphin. A good figure of such a specimen is given by G. ST HILAIRE, *Hist. des Anom.*, ed. 1837, I. p. 96, where a full account of the older literature of the

[1] C. DARWIN, *Animals and Plants under Domestication*, 2nd edition, I. p. 92.
[2] *Ibid.*, p. 93, *note*.

subject may be found. Inasmuch as carp are largely bred in ponds on the continent, there is in this case some suggestion that unnatural conditions may be concerned, but this suggestion does not apply to other cases of the same Variation. OTTO, *Lehrb. path. Anat.*, I. § 129, states that in the ponds of Silesia such fish are not rare. See also VOIGT, *Mag. f. d. Naturk.*, III. p. 515.

Cyprinus hungaricus: specimen from the Danube similarly formed. The forehead was protuberant and bulged in front of the eyes so that its anterior border was almost vertical. The attachments of the mandible are carried forward in such a manner that the mandible *itself was directed upwards almost at right angles to the body. [Good* figure.] STEINDACHNER, *Verh. zool.-bot. Ges. Wien*, 1863, XIII. p. 485, *Plate.*

[Several other types of Variation in the heads of Cyprinoids occur, but cannot be described here.]

CHUB (*Leuciscus dobula = cephalus*) : specimen having anterior part of head rounded "like a monumental dolphin." The body was normal, measuring 33 cm. in length. LANDOIS, *Zool. Garten*, 1883, XXIV. p. 298.

MINNOW (*Phoxinus lævis*) specimen having a snout like a pug ("*museau du mopse*") [no description]. LUNEL, *Poiss. du lac Léman*, p. 96.

MULLET (*Mugil capito*): specimen having both jaws directed upwards, and the upper and anterior parts of the skull greatly elevated and protuberant: the appearance of the head was like that of a pug dog. Full measurements given. CANESTRINI, R., *Atti della soc. Ven.—Trent. di. sci. nat. in Padova*, 1884, IX. p. 117 [Bibliography given].

PIKE (*Esox lucius*) described as like a pug, *ibid.*, p. 124; see also VROLIK'S *Atlas*, 1849, *Tab* LXI. *fig.* 6.

SALMON (*Salmo salar*): specimen having front part of face little developed, the supra-maxillaries being asymmetrical. Lower jaw projects far in front of upper jaw. Animal of fair size, and not meagre. VAN LIDTH DE JEUDE, *Notes from Leyden Mus.*, VII. p. 259, *Plate.* [Curious malformation of *S. trutta* ibid.], see also *Jahrb. Ver. vaterl. Nat. Württ.* XLII. p. 345.

TROUT (*S. fario*): several specimens having bull-dog heads were taken in Lochdow, near Pitmain, Inverness-shire. Heads short and round; upper iaw truncated like a bull-dog. This variety does not

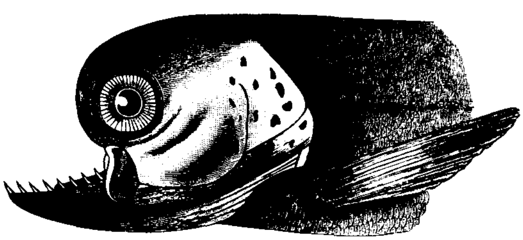

FIG. 6. Bull-dog-headed TROUT after CARLET.

occur in neighbouring lochs. None weighed more than ½ lb. YARRELL, *Brit. Fishes*, I. p. 286, figure given.

Another specimen (Fig. 6), agreeing closely with Yarrell's figure, was taken in a lake at an altitude of over 6000 ft. in the valley of Sept-Laux (Isère). Saving the head it was in all respects normal. This specimen is described and figured by CARLET, M. G., *Journ. de l'Anat. et Phys.*, 1879, XV. p. 154. [It is declared that the fishermen who took it, having previously met with similar specimens, supposed that they had found a new species, but it is not expressly stated that these other specimens were from the same locality.]

Before ending this preliminary glance at Discontinuity in Substantive Variation, allusion must be made to a case which is at once more famous and more instructive than any other. I refer to the celebrated phenomenon of the production of nectarines by peaches, or conversely. Upon the subject of almond, peach and nectarine, Darwin produced a body of facts which, whether as an example of a method or for the value of the facts themselves, form perhaps the most perfect and the most striking of all that he gave.

The evidence which is there collected is known to all, and though similar observations have been made since by many, there is I believe nothing of importance to add to Darwin's statement. The bearing of these phenomena on the nature of Discontinuity in Variation is so close that Darwin's summary may with profit be given at length.

"To sum up the foregoing facts; we have excellent evidence of peach-stones producing nectarine-trees, and of nectarine-stones producing peach-trees—of the same tree bearing peaches and nectarines—of peach-trees suddenly producing by bud-variation nectarines (such nectarines reproducing nectarines by seed), as well as fruit in part nectarine and in part peach,—and, lastly, of one nectarine-tree first bearing half-and-half fruit and subsequently true peaches"[1]. After disposing of alternative hypotheses he concludes that "we may confidently accept the common view that the nectarine is a variety of the peach, which may be produced either by bud-variation or from seed."

In this case the evidence is complete. The variation from peach to nectarine or from nectarine to peach may be *total*. If less than total, the fruit may be divided into either halves or quarters[2], so that for each segment the Variation is total still. Of intermediate forms other than these divided ones, we have in this case

[1] *Animals and Plants under Domestication*, ed. 2, I. p. 362.

[2] *Ibid.*, p. 362, quoting from *Loudon's Gard. Mag.* 1828, p. 53. The case of a Royal George peach which produced a fruit, "three parts of it being peach and one part nectarine, quite distinct in appearance as well as in flavour." The lines of division were longitudinal.

no evidence: it is therefore a fair presumption that they are either rare or non-existent; and that the peach-state and the nectarine-state are thus positions of "Organic Stability," between which the intermediate states, if they are chemical and physical possibilities, are positions of instability.

These examples of Discontinuity in Substantive Variation must suffice to illustrate the nature of the phenomena. It will be seen that the matters touched on cover a wide range, and the evidence relating to them must be considered separately and at length. Such a consideration I hope in a future volume to attempt.

SECTION XI.

DISCONTINUITY IN MERISTIC VARIATION: EXAMPLES.

Inasmuch as the facts of Meristic Variation form the substance of this volume, it is unnecessary in this place to do more than refer to the manner in which they exhibit the phenomenon of Discontinuity. One or two instances must suffice to give some suggestion of this subject, detailed consideration being reserved.

Parts repeated meristically form commonly a series, which is either radial or linear, or disposed in some other figure derived from or compounded of these. For the purpose of this preliminary treatment an instance of Discontinuous Variation in each of these classes may be taken.

1. *Radial Series.*

Variations in the number of petals of actinomorphic flowers exhibit the Discontinuity of Meristic Variation in perhaps its simplest form.

Phenomena of precisely similar nature will hereafter be described in animals, but such variations in flowers are so common and so accessible that reference to them may with profit be made. In Fig. 7 such an example is shewn.

It represents a Tulip having the parts of the flower formed in multiples of four, instead of in multiples of three as normally. Variation of this kind may be seen in any field or hedgerow[1].

Meristic Variation is here presented in its greatest simplicity. Such a case may well serve to illustrate some of the phenomena of Discontinuity.

[1] For full literature and lists of cases see especially MASTERS, *Vegetable Teratology*, s. v. *Polyphylly*. It is perhaps unnecessary to refer to the fact that the numerical changes here spoken of are quite distinct from those which result from an assumption by the members of one series or whorl of the form and characters proper to other whorls.

A form with four segments occurs as the offspring of a form with three segments. Such a Variation, then, is discontinuous

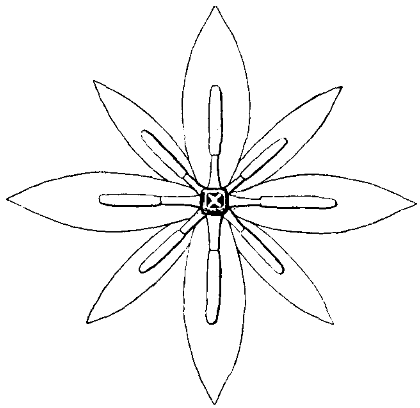

FIG. 7. Diagram of the flower of a Tulip having all the parts in -4.

because a new character, that of division into four, has appeared in the offspring though it was not present in the parent. This new character is a definite one, not less definite indeed than that of division into three. It has come into the strain at one step of Descent. Instances in which there is actual evidence of such descent are rare, but there can be no question that these changes do commonly occur in a single generation, and, indeed, in many plants, as for example *Lysimachia* (especially *L. nemorum*), flowers having all the parts in -4 or in -6 may be frequently seen on plants which bear likewise normal flowers with the parts in -5.

Now such a variation as this of the Tulip illustrates a phenomenon which in the Study of Variation will often be met.

We have said that the variation is discontinuous, meaning thereby that the change is a large and decided one, but it is more than this; it is not only large, it is *complete.*

The resulting form possesses the character of division into four no less completely and perfectly than its parent possessed the character of division into three. The change from three to four is thus perfected: from the form with perfect division into three is sprung a form with perfect division into four. This is a case of a *total* or *perfect* Variation.

This conception of the totality or perfection of Variation is one which in the course of the study will assume great importance, and it may be best considered in the simple case of numerical and Meristic Variation before approaching the more complex question of the nature of totality or perfection in Substantive Variation.

The fact that a variation is perfect at once leads to the question as to what it might be if imperfect. Between the form in -3 and the form in -4 are intermediates possible? and if possible, do they exist? Now by choosing suitable species of regular flowers, individual flowers may no doubt be found in which there are three large segments and one small one; or two normal segments and a third divided into two, making four in all. Such flowers are firstly rare, while cases of perfect transformation are common. But besides their rarity there is, further, a grave doubt whether they are in any true sense *intermediate* between the perfect form in -3 and the perfect form in -4. After this again it must be asked whether or no they do as a matter of fact occur as intercalated steps in the descent of the form in -4 from the form in -3? To the last question a general negative may at once be given; for though there is abundant evidence that Meristic Variations of many kinds and in several degrees of completeness may be seen in the offspring of the same parent, yet any one member of such a family group may shew a particular Variation in its perfection, and the occurrence of any intermediate in the line of Descent is by no means necessary for the production of the perfect Variation.

To answer the former question, whether or no forms imperfectly divided into four parts are in reality intermediate between those in -3 and those in -4, a knowledge of the mechanics of the process of Division is required. Such knowledge is as yet entirely wanting, and discussion of this matter must therefore be premature. With much hesitation I have decided to make certain reflexions on the subject, which will be found in an Appendix to this work. These may perhaps have a value as suggestions to others, though from their theoretical nature they can find no place here.

There is however another class of cases which are intermediate in a different way. In the Tulip described above the quality of division into 4 was present in all the floral organs. This is not always the case, for a Meristic Variation may be present in one series of organs, though it is absent in some or all of the others, and this is a phenomenon frequently recurring. Nevertheless, though only partially distributed, a Variation may still be displayed in its totality in the parts wherein it is present. The parts of a single whorl, the calyx for example, may undergo a complete Variation, while the corolla and other parts are unchanged. In the same way single members of a radial series, as a petal for example, may undergo a complete Variation while the other members of the series are unchanged. The same will be shewn hereafter to be true of animals also.

For instance, the normal number of the parts in the disc of *Aurelia* is four, but the whole body may be divided instead into six or some other number of parts. Examples are also found in which the parts of one-half or of one quadrant are arranged in the new number, while the remainder is normal; and, as in flowers, this new number may prevail in some or in all of those systems of organs which are disposed around the common centre.

2. *Linear Series.*

Before speaking further of the totality or perfection of Variation it will be well to give an illustration of Discontinuous Meristic Variation as it occurs in the case of a linear series of parts. As such an illustration the case of the variation in the number of joints in the tarsus of the Cockroach (*Blatta*) may be taken. This variation has been the subject of very full investigation by Mr H. H. Brindley. The tarsus of the Cockroach is normally divided into five joints, but in about 25 per cent. of *B. americana* (and in a smaller proportion of several other species) the tarsus of one or more legs is divided into only four joints, though the total length may be the same as that of the corresponding leg of the other side, Fig. 8. Between the five-jointed form of tarsus and the four-jointed form no single case in any way intermediate was seen. The whole

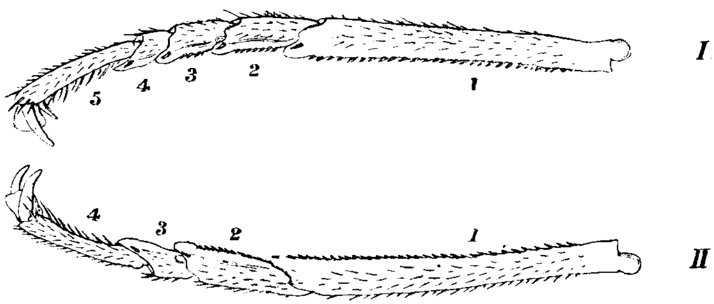

FIG. 8. Tarsi of the third pair of legs in a specimen of *Blatta americana*, I. the left tarsus, having the normal, or 5-jointed form; II. the right tarsus, having the 4-jointed form.

evidence will be given in full in the proper place and raises many questions of great interest; but that which is important to our present consideration is the fact that the Variation is here undoubtedly discontinuous, arising suddenly as a total or perfect Variation, from the five-jointed form to the four-jointed. Here the variation, though total as regards the limb in which it is present, is not total as regards all the legs taken together. For commonly only a single leg had a four-jointed tarsus, and only one specimen was met with in which all six legs thus varied, and one specimen only shewed the variation in five legs.

In speaking of such a Variation as a *perfect* Variation several things are meant.

First, it is meant that the tarsus of the new pattern is as distinctly divided into four joints as the normal is into five. In addition to this the statement that the varying limb is perfect conveys a number of ideas that cannot be readily formulated; for example, that the joints are to all appearance properly proportioned and serviceable, shewing no sign of unfitness: they have in fact much the same appearance as they have in those of the Orthoptera in which the tarsus is normally four-jointed. But besides these attributes, which though useful enough for ordinary description are still in their nature formless and of no precise application, there is another which in the case of these varying legs we are entitled to make. We have said that these four-jointed tarsi are to all appearance normal, save for the number of the joints. Now the measurements which, at my suggestion, Mr Brindley has been kind enough to make, entitle us to go beyond this, and to assert that the four-jointed tarsus has another character by reason of which it is actually in a sense a "normal" form. A brief consideration of this will clearly illustrate the meaning of the term "perfection" applied to Variation.

We saw above that in a monomorphic form, the frequency with which, in respect of any given character, it departs from its mean condition follows a curve of Frequency of Error. This is, indeed, what is meant by the statement that the mean condition is a normal.

Taking the five-jointed tarsus, measurements shewed that the ratio of the length of any given joint to the length of the whole tarsus varied in this way about a mean value. Measurement of the joints of the four-jointed form shewed that the ratios which they bear to the total length of their respective tarsi vary in a similar way about their mean values, and that there is thus a "normal" four-jointed condition just as there is a "normal" five-jointed condition. In the same way, then, that the ratio of the length of each of the five joints to that of the whole tarsus is not always identical but exhibits small variations, so the ratios of the several joints of the four-jointed tarsus to the length of the whole tarsus also vary, but in each case the ratio has a mean value which is approached with a frequency conforming to a curve of Error.

The measurements established also another fact which is of consequence to an appreciation of the nature of totality in Variation. It not only appeared that the departures from the mean value of these ratios in the four-jointed variety were distributed about the mean in the same way as those of the five-jointed form, but it was also shewn that the absolute variations from the mean values of these ratios were not on the whole greater in the four-jointed tarsi than in the five-jointed tarsi. In other words, the four-jointed tarsus occurring thus sporadically, as a variety, is not less definitely constituted than the five-jointed type, and the proportions of its several joints *are not less constant. It is scarcely necessary to point out that* these facts give no support to the view that the exactness or perfection with which the proportions of the normal form are approached is a consequence of Selection. It appears rather, that there are two possible conditions, the one with five joints and the other with four, either being a position of Organic Stability. Into either of these the tarsus may fall; and though it is still conceivable that the final choice between these two may have been made by Selection, yet it cannot be supposed that the accuracy and completeness with which either condition is assumed is the work of Selection, for the "sport" is as definite as the normal.

This interesting case of Meristic Variation in the tarsus of the Cockroach illustrates in a striking way the principle which is perhaps the chief of those to which the Study of Variation at the outset introduces us. We are presented with the phenomenon of an organ existing in two very different states, between which no intermediate has been seen. Each of these states is definite and in a sense perfect and complete; for the oscillations of the four-jointed form around its mean condition are not more erratic than those of the normal form. Now when it is remembered that just such a four-jointed condition of the tarsus is known as a normal character of many insects and especially of some Orthoptera, it is, I think, difficult to avoid the conclusion that if the four-jointed groups are descended from the five-jointed, the Variation by which this condition arose in them was of the same nature as that seen as an individual Variation in *Blatta*; that as the modern phenomenon of the individual Variation which we see, so that past phenomenon of the birth of a four-jointed race, was definite and complete, and that the change whose history is gone, like the change to be seen to-day, was no gradual process, but a Discontinuous and total Variation[1].

[1] Since this Section was written it has seemed possible that the account given above may be found to need an important modification. It is well known that *Blatta*, in common with many other Orthoptera, has the power of reproducing the antennæ and legs after amputation or injury, and we have made some observations shewing that the tarsi of these regenerated legs sometimes, if not always, contain *four* joints. The question therefore arises whether the 4-jointed tarsus is a truly congenital variation, and not rather a variation introduced in the process of regeneration, somewhat after the manner of a bud-variation. To determine this point a considerable number of immature specimens were examined, and it was found that the percentage of individuals with 4-jointed tarsi is considerably less in the young than in the adult. These facts lend support to the view that the 4-jointed condition is not congenital. A quantity of individuals were also hatched from the egg-cocoons, and among them there has thus far been found no case of 4-jointed tarsus. On the other hand the total number thus hatched is not yet sufficient to create any strong probability that none are ever hatched in the 4-jointed state. We have also seen the 4-jointed tarsus in three very young individuals, which, to judge from their total length, must have been newly hatched. The statistics shew besides that the abnormality is distinctly commoner in females than in males, and that it is commoner in the legs of the 2nd pair than in the 1st, and much more common in the 3rd pair of legs than in the 2nd. These facts somewhat favour the view that the variation may be congenital. It seems also exceedingly improbable that in the specimen with all the tarsi 4-jointed, the six legs could each have been lost and renewed. There seems on the whole to be a pre-

SECTION XII.

Parallel between Discontinuity of Sex and Discontinuity in Variation.

The application of the term Discontinuity to Variation must not be misunderstood. It is not intended to affirm that in discontinuous Variation there can be between the variety and the type no intermediate form, or that none has been known to occur, and it is not even necessary for the establishment of Discontinuity that the intermediate forms should be rare relatively to the perfect form of the variety, though in cases of discontinuous Variation this is generally the case; but it is rather meant that the perfect form of the variety *may* appear at one integral step in Descent, either without the occurrence of intermediate gradations, or at least without the intercalation of such graduated forms in the pedigree.

In the case of the tarsus of *Blatta* we have seen an example of a total and complete Variation affecting single members of a series of repeated parts, not collectively, but one or more at a time[1]. Such an instance of a Meristic Variation occurring in a state which is total as regards members of a series but not total as regards the whole series finds many parallels among Substantive Variations, as, for example, that of the Crab (*Cancer pagurus*) bearing the right third maxillipede fashioned as a chela, while the left third maxillipede was normal. Variations of this nature in plants are of course well known to all.

At a previous place (Section VII.) allusion was made to the familiar but very curious analogy between members of a series of Meristic parts and separate organisms. The facts of Variation bring out this analogy in many singular ways, and in speaking of the totality of Variation it is necessary to bear these facts in mind. Not only are there abundant instances of independent division or multiplication of single members of Meristic series, but as has been said, single members of such series may thus independently and singly undergo qualitative or Substantive Variation, being treated in the physical system of the body as though they were separate units. In Variation, therefore, though it will be

sumption that the variation may at least sometimes be congenital. Supposing however that this shall be found hereafter not to be the case, I do not think that the deductions drawn from the facts will be less valid. The conclusions as to the definiteness of the two types, and the relationships of the several parts of each to the several parts of the other, would still hold good. There are besides in other forms, instances of similar numerical Variation, as for example, in the number of joints in the antennæ of Prionidæ, where the hypothesis of change on renewal is impossible, from which a similar argument might be drawn; but on the whole I have preferred to leave the account as it stands, taking the case of *Blatta* as an example, because it is easily accessible and because, from the fewness of the joints concerned, the issues are singularly clear.

[1] See *Note at the end of Section* XI.

found that members of Meristic series *may* vary simultaneously and collectively—and this is one of the most important generalizations which result from the Study of Variation—yet it is also true that in Variation single members of such series *may* vary independently and behave as though they possessed an "individuality" of their own. If ever it shall be possible to form a conception of the physical processes at work in the division and reproduction of organisms, account must be taken of both of these phenomena.

I know no way in which the nature of Discontinuity in Variation and the position of intermediate forms may be so well illustrated as by the closely parallel phenomenon of Sex. In the case of Sex in the higher animals we are familiar with the existence of a race whose members are at least dimorphic, being formed either upon one plan or upon the other, the two plans being in ordinary experience alternative and mutually exclusive. Between these two types, male and female, there are nevertheless found intermediate forms, "hermaphrodites," occurring in the higher animals at least, as great rarities. Now though these intermediate forms perhaps exist in gradations sufficiently fine to supply all the steps between male and female, it cannot be supposed that the one sex has been derived from the other, and still less that the various stages of hermaphroditism have been passed through in such Descent. Besides this, even though there is an accurate correspondence or homology between the several organs which are modified upon the one plan in the male and upon another in the female, and though this homology is such as to suggest, were we comparing two species, that the one had been formed from the other, part by part, yet by the nature of the case such a view is here inadmissible: for firstly it is impossible to suppose that either sex has at any time had the organs of the other in their completeness, and secondly it is clear that any hypothetical common form, by modification of which both may have arisen, must have been indefinitely remote and could certainly not have possessed secondary sexual organs bearing any resemblance to those now seen in the higher forms. All this has often been put, but the application of it to Variation is of considerable value. For in the case of Sex there is an instance of the existence of two normals and of many forms intermediate between them, occurring in a way which precludes the supposition that the intermediates represent stages that have ever occurred in the history of the two forms.

In yet another way Sex supplies a parallel to Variation. As we know, the sexes are discontinuous and occur commonly in their total or perfect forms. Now just as members of a Meristic series may present total variations independently of each other, so may single members of such a series present opposite secondary sexual characters, which may nevertheless be in each case complete.

The best known instance of this is that of gynandromorphic insects, in which the characters of the whole or part of one side of the body, wings and antennæ, are male, while those of the other side are female. Remarkable instances of a similar phenomenon have been recorded among bees and will be described later. As is well known, the organs and especially the legs of the sexless females or workers are formed differently from those of the drones, but there are cases of individuals having some of the parts and appendages formed on the one plan and some on the other. Thus in these individuals, which are in a sense intermediate between workers and drones, the characters of the two sexes may still be not completely blended, the male type prevailing in some parts, and the female in others. In the Discontinuity of Substantive Variation will be found examples of imperfect blending of variety and type closely comparable with this case of the imperfect blending of Sex.

SECTION XIII.

SUGGESTIONS AS TO THE NATURE OF DISCONTINUITY IN VARIATION.

The observations at the end of Section XI, regarding the Discontinuity of Meristic Variation lead naturally to certain reflexions as to the nature of Discontinuous Variation in general. In the case of the Cockroach tarsus, there given, it appeared that just as the structure of the typical form varies about its mean condition, so the structure of the variety varies about another mean condition. This fact, which in the given instance of Meristic Variation is so clear, at once suggests an inquiry whether this is not the usual course of Discontinuous Variation, and, indeed, whether Discontinuity in Variation does not mean just this, that in varying the organism passes from a form which is the normal for the type to another form which is a normal for the variety. Such transitions plainly occur in many cases of Meristic Variation, and in a considerable number of Substantive Variations there will be found to be indications that the phenomenon is similar. It is true that at the present stage of the inquiry the evidence has the value rather of suggestion than of proof, but the suggestion is still very decided and it is scarcely possible to exaggerate the importance of even this slender clue.

In stating the problem of Species at the beginning of this inquiry it was said that the forms of living things, as we know them, constitute a discontinuous series, and it is with the origin of the Discontinuity of the series that the solution of the main problem is largely concerned. Now the evidence of Discontinuous Variation suggests that organisms may vary abruptly from the *definite form of the type to a form of variety which has also in* some measure the character of definiteness. Is it not then possible that the Discontinuity of Species may be a consequence and expression of the Discontinuity of Variation? To declare at the present time that this is so would be wholly premature, but the suggestion that it is so is strong, and as a possible light on the whole subject should certainly be considered.

In view of such a possible solution of one of the chief parts of the problem of Species it will be well to point out a line of inquiry which must in that event be pursued. If it can be shewn that the Discontinuity of Species depends on the Discontinuity of *Variation, we shall then have to consider the causes of the Dis*continuity of Variation.

Upon the received hypothesis it is supposed that Variation is continuous and that the Discontinuity of Species results from the operation of Selection. For reasons given above (pp. 15 and 16) there is an almost fatal objection in the way of this belief, and it cannot be supposed both that all Variation is continuous and also that the Discontinuity of Species is the result of Selection. With evidence of the Discontinuity of Variation this difficulty would be removed.

It will be noted also that it is manifestly impossible to suppose that the perfection of a variety, discontinuously and suddenly *occurring, is the result of Selection.* No doubt it is conceivable that a race of Tulips having their floral parts in multiples of four might be raised by Selection from a specimen having this character, but it is not possible that the perfection of the nascent variety can have been gradually built up by Selection, for it is, in its very beginning, perfect and symmetrical. And if it may be seen thus clearly that the perfection and Symmetry of a variety is not the work of Selection, this fact raises a serious doubt that perhaps the similar perfection and Symmetry of the type did not owe its origin to Selection either. This consideration of course touches only the part that Selection may have played in the first building up of the type and does not affect the view that the perpetuation of the type once constituted, may have been achieved by Selection.

But if the perfection and definiteness of the type is not due to Selection but to the physical limitations under which Variation proceeds, we shall hope hereafter to gain some insight into the nature of these limitations, though in the present state of zoological study the prospect of such progress is small. In the observations which follow I am conscious that the bounds of profitable speculation are perhaps exceeded, and I am aware that to many this may seem matter for blame; but there is, in my judgment, a plausibility in the views put forward, sufficient at least to entitle them to examination. They are put forward in no sense as a formulated theory, but simply as a suggestion for work. It is, besides, only in foreseeing some of the extraordinary possibilities that lie ahead in the Study of Variation, that the great value of this method can be understood.

It has been seen that variations may be either Meristic or Substantive, and that in each group discontinuous and definite variations may occur by steps which may be integral or total. We are now seeking the factors which determine this totality and define the forms assumed in Variation. In this attempt we may, by arbitrarily confining our first notice to very simple cases, recognize at least two distinct factors which may possibly be concerned in this determination. *Of these the first relates to Meristic* Variation and the second to Substantive Variation.

1. *Possible nature of the Discontinuity of Meristic Variation.*

Looking at simple cases of Meristic Variation, such as that of the Tulip or of *Aurelia*, or of the Cockroach tarsus, there is, I think, a fair suggestion that the definiteness of these variations is determined *mechanically*, and that the patterns into which the tissues of animals are divided represent positions in which the forces that effect the division are in equilibrium. On this view, the lines or planes of division would be regarded as lines or planes at right angles to the directions of the dividing forces; and in the lines of Meristic Division we are perhaps actually presented with a map of the lines of those forces of attraction and repulsion which determine the number and positions of the repeated parts, and from which Symmetry results. If the Symmetry of a living body were thus recognized as of the same nature as that of any symmetrical system of mechanical forces, the definiteness of the symmetry in Meristic Variation would call for no special remark, and the perfection of the symmetry of a Tulip with its parts divided into four, though occurring suddenly as a "sport," would be recognized as in nowise more singular than the symmetry of the type. Both alike would then be seen to owe their perfection to mechanical conditions and not to Selection or to any other gradual process. If reason for adopting such a view of the physics of Division should appear, the frequency with which in any given form a particular pattern of Division or of Symmetry recurs, would be found to be determined by and to be a measure of the stability of the forces of Division when disposed in that particular pattern. It will of course be understood that in these remarks no suggestion is offered as to the causes which determine whether a tissue shall divide into four or into three, but merely as to the conditions of perfection of the division in either case. It will also be clear that though the symmetry of a flower or of any other tissue depends also on symmetrical growth, it is primarily dependent on the symmetry of its primary divisions, upon which symmetrical growth and secondary symmetrical divisions follow.

It would be interesting and I believe profitable to examine somewhat further the curiously close analogy between the symmetry of bodily Division and that of certain mechanical systems by which close imitations both of linear and of radial segmentation can be produced; and though to some this might seem overdaring, the possibility that the mechanics of bodily Division are in their visible form of an unsuspected simplicity is so far-reaching that it would be well to use any means which may lead others to explore it.

And even if at last this suggestion shall be found to have in it no other element of truth, it would still be of use as a forcible presentation of the fact, which when realized can hardly be doubted, that among the factors which combine to form a living body, the forces of Division may be distinguished as in their manifestations separable from the rest and forming a definite group. For, already (Section v.) it has been pointed out that the patterns of Division or Merism may be changed, while the Substance of the tissues presents to our senses no difference. The recognition of this essential distinctness of the Meristic forces will, I believe, be found to supply the base from which the mechanics of growth will hereafter be attacked.

The problems of Morphology will thus determine themselves into problems in the physiology of Division, which must be recognized together with Nutrition, Respiration and Metabolism, as a fundamental property of living protoplasm.

To sum up: there is a possibility that Meristic Division may be a strictly *mechanical* phenomenon, and that the perfection and Symmetry of the process, whether in type or in variety, may be an expression of the fact that the forms of the type or of the variety represent positions in which the forces of Division are in a condition of Mechanical Stability.

2. *Possible nature of the Discontinuity of Substantive Variation.*

Passing from the phenomena of Division and arrangement to those of constitution or substance we are, as has been said, again presented with the phenomenon of discontinuous or total Variation, and we must seek for causes which may perhaps govern and limit this totality, and in obedience to which the Variation is thus definite. Now as in the case of Meristic Variation, by arbitrarily limiting the examination to those cases which seem the simplest it appears that there is at least an analogy between them and certain mechanical phenomena, so by similarly restricting ourselves to very simple cases there will be seen to be a similar analogy between the discontinuity of some Substantive Variations and that of *chemical* discontinuity. It is on the whole not unreasonable to expect that the definiteness of at least some Substantive Variations depends ultimately on the discontinuity of chemical affinities. To take but one instance, that of colour, we are familiar with the fact that the colours of many organic substances undergo definite changes when chemically acted on by reagents, and it is not suggested that the definiteness and discontinuity of the various colours assumed is dependent on anything but the definiteness of the chemical changes undergone. The changes of litmus and many vegetable blues to red on treatment with acids, of many vegetable yellows to brown on treatment with alkalies, the colours of the series of bodies produced by the progressive oxidation of biliverdin are familiar examples of such definite colour-variations.

With facts of this kind in view, the conclusion is almost forced on us that the definiteness of colour-variation is a consequence of the definiteness of the chemical changes undergone. No one doubts that the orange colouring matter of the variety of the Iceland Poppy (*P. nudicaule*) is a chemical derivative from the yellow colouring matter of the type. It is not questioned that in such cases a definite alteration in the chemical conditions in which the pigment is produced determines whether the flower shall be orange or yellow; and I think it is reasonable to expect that the frequency with which the flowers are either yellow or orange as compared with the rarity of the intermediate shades is an expression of the fact that the yellow and orange forms of the colouring matter have a greater chemical stability than the intermediate forms of the pigment, or than a mixture of the two pigments. If then it should happen, as we may fairly suppose it might, that the orange form were to be selected and established as a race, it would owe the definiteness of its orange colour and the precision of its tint, not to the precision with which Selection had chosen this particular tint, but to the chemical discontinuity of which the originally discontinuous Variation was the expression.

To pass from the case of a sport to that of Species, it is well known that of the many S. African butterflies of the genus *Euchloe* (= *Anthocharis*, Orange-tips), some have the apices or tips of the fore-wings orange-red (for example, *E. danae*), while in others they are purple (for example, *E. ione*). Upon the view that the transition from orange to purple, or *vice versa*, had been continuously effected by the successive Selection of minute variations, we are met by all the difficulties we know so well. Why is purple a good colour for this creature? If purple is a good colour and red is a good colour, how did it happen that at some time or other all the intermediate shades were also good enough to have been selected? and so on. These and all the cognate difficulties are opened up at once, and though they have been met in the fashion we know, they have scarcely been overcome. But at the outset this view assumes that every intermediate may exist and has existed, an assumption which is gratuitous and hardly in accordance with the known fact that chemical processes are frequently discontinuous. When besides this it is known that Variation *may* be discontinuous, I submit that it is easier to suppose that the change from red to purple was from the first complete, and that the choice offered to Selection was between red and purple; and that the tints of the purple and of the red were determined by the chemical properties of the body to which the colour is due. This case is a particularly interesting one in the light of the fact that, as Mr F. G. Hopkins has lately shewn me, this purple colour, dissolved in hot water, leaves on evaporation a substance which gives the murexide reaction and cannot as yet be distinguished from the substance similarly derived from the orange or yellow colouring matters of Pieridæ in general. As was stated above, Mr Hopkins has shewn that these yellows are acids, allied to mycomelic acid, a derivative of uric acid, and therefore of the nature of excretory products. Whether the purple body is related to the yellow or to the orange as a salt is to an acid, or otherwise, cannot yet be affirmed; but if the difference between them is a chemical difference, which can hardly be doubted, there is at least a presumption that the discontinuity of these colours in the several species, is an expression of the discontinuity of the chemical properties of this body. The possibility that from such bodies a series of substances might perhaps by suitable means be prepared in such a way as to represent many or even all intermediate shades, does not greatly affect the suggestion made; for even in such series it is almost certain that points of comparative stability would occur, and Discontinuity would be thus introduced.

The case of Colour has been taken in illustration because it is the simplest and most intelligible example of the possibility that the Discontinuity of some Substantive Variations is determined by the Discontinuity of the chemical processes by which the structures are produced. It is true that perhaps no species has been rightly differentiated by colour alone, but colour is still one of the many characters which go to the distinguishing of a species, and it is precisely one of the characters whose significance and delimitation by Natural Selection is most obscure. Moreover by the fact that in the case of these yellow and red Pieridæ the colours are of an excretory nature, we are reminded that Variation in colour may be an index of serious changes in the chemical economy of the body, and that when an animal is said to be selected because it is red or because it is purple, the real source of its superiority may be not its red colour or its purple colour, but other bodily conditions of which these colours are merely symptoms. By those who have attempted to reconcile the phenomena of Colour with the hypothesis of Natural Selection this fact is too often overlooked.

But though it may reasonably be supposed that much of the Discontinuity of Variation and some of the Discontinuity of

Species arise through discontinuous transition from one state of mechanical or chemical stability to another state of stability, there nevertheless remain large classes of discontinuous variations, and of Specific Differences still more, whose Discontinuity bears no close analogy with these. To these phenomena inorganic Nature offers no parallel. We may see that they are discontinuous and that their course is in some way controlled, but as to the nature of this control we can make no guess.

Though the resemblance may be misleading, it is nevertheless true that in *living* Nature there are other phenomena, those of disease, which present a Discontinuity closely comparable with that of many variations. In problems of disease we meet again the same problem which we meet in Variation, namely, changes which may be complete or specific, though occurring so suddenly as to exclude the hypothesis that Selection has been the limiting cause. All this is familiar to everyone who has considered the problem of Species.

For though, like discontinuous variations, the manifestations of specific disease are not always identical, but differ in intensity and degree, varying about a normal form, still these manifestations may be specific in the sense in which the term is used with reference to the characters of Species. If we exclude those diseases whose specific characters are now known to be the result of the invasion of specific organisms, there still remain very many which are known and recognized by definite and specific symptoms produced in the body, though there is as yet no evidence that they are due to specific organisms. [Of course if it were shewn that these diseases also result from the action of specific organisms, they then only present to us again the original problem of Species; for if the definiteness, or Species, of a disease is due to the definiteness, or Species, of the micro-organism which causes it, the cause of that definiteness of the micro-organism remains to be sought, and we are simply left with a particular case of the general problem of Species.] But in the meantime we can see that the manifestations are specific; and while we do not know that they result from causes themselves specific, the nature of the control in obedience to which they are specific is unknown.

The parallel between disease and Variation may be misleading, but this much at least may fairly be learned from it: that the system of an organized being is such that the result of its disturbance may be specific. And in the end it may well be that the problem of Species will be solved by the study of pathology; for the likeness between Variation and disease goes far to support the view which Virchow has forcibly expressed, that "every deviation from the type of the parent animal must have its foundation on a pathological accident[1]."

[1] R. VIRCHOW, *Journal of Pathology*, I. 1892, p. 12.

SECTION XIV.

SOME CURRENT CONCEPTIONS OF BIOLOGY IN VIEW OF THE FACTS OF VARIATION.

Enough has now been said to explain the aim of the Study of Variation, and to shew the propriety of the choice of the facts of Meristic Variation as a point of departure for that study. Before leaving this preliminary consideration, reference to some cognate subjects must be made.

It has been shewn that in view of the facts of Variation, some conceptions of modern Morphology must be modified, while others must be abandoned. With the recognition of the significance of the phenomena of Variation, other conceptions of biology will undergo like modifications. As to some of these a few words are now required, if only to explain methods adopted in this work.

1. *Heredity.*

It has been the custom of those who have treated the subject of Evolution to speak of "Heredity" and "Variation" as two antagonistic principles; sometimes even they are spoken of as opposing "forces."

With the Study of Variation, such a description of the processes of Descent will be given up, even as a manner of speaking. In what has gone before I have as far as possible avoided any use of the terms Heredity and Inheritance. These terms which have taken so firm a hold on science and on the popular fancy, have had a mischievous influence on the development of biological thought. They are of course metaphors from the descent of property, and were applied to organic Descent in a time when the nature of the process of reproduction was wholly misunderstood. This metaphor from the descent of property is inadequate chiefly for two reasons.

First, by emphasizing the fact that the organization of the offspring depends on material transmitted to it by its parents, the metaphor of Heredity, through an almost inevitable confusion of thought, suggests the idea that the actual body and constitution of the parent are thus in some way handed on. No one perhaps would now state the facts in this way, but something very like this material view of Descent was indeed actually developed into Darwin's Theory of Pangenesis. From this suggestion that the body of the parent is in some sort remodelled into that of the offspring, a whole series of errors are derived. Chief among these is the assumption that Variation must necessarily be a continuous process; for with the body of the parent to start from, it is hard to conceive the occurrence of discontinuous change. Of the deadlock which has resulted from the attempt to interpret Homology on this view of Heredity, I have already spoken in Section VI.

Secondly, the metaphor of Heredity misrepresents the essential phenomenon of reproduction. In the light of modern investigations, and especially those of Weismann on the continuity of the germ-cells, it is likely that the relation of parent to offspring, if it has any analogy with the succession of property, is rather that of trustee than of testator.

Hereafter, perhaps, it may be found possible to replace this false metaphor by some more correct expression, but for our present purpose this is not yet necessary. In the first examination of the facts of Variation, I believe it is best to attempt no particular consideration of the working of Heredity. The phenomena of Variation and the *origin* of a variety must necessarily be studied first, while the question of the perpetuation of the variety properly forms a distinct subject. Whenever in the cases given, observations respecting inheritance are forthcoming they will be of course mentioned. But speaking of discontinuous Variation in general, the recurrence of a variation in offspring, either in the original form or in some modification of it, has been seen in so many cases, that we shall not go far wrong in at least assuming the possibility that it *may* reappear in the offspring. At the present moment, indeed, to this statement there is little to add. So long as systematic experiments in breeding are wanting, and so long as the attention of naturalists is limited to the study of normal forms, in this part of biology which is perhaps of greater theoretical and even practical importance than any other, there can be no progress.

2. *Reversion.*

Around the term Reversion a singular set of false ideas have gathered themselves. On the hypothesis that all perfection and completeness of form or of correlation of parts is the work of Selection it is difficult to explain the discontinuous occurrence of new forms possessing such perfection and completeness. To account for these, the hypothesis of Reversion to an ancestral form is proposed, and with some has found favour. That this suggestion is inadmissible is shewn at once by the frequent occurrence by discontinuous Variation, of forms which though equally perfect, cannot all be ancestral. In the case of *Veronica* and *Linaria*, for example, a host of symmetrical forms of the floral organs may be seen occurring suddenly as sports, and of these though any *one* may conceivably have been ancestral, the same cannot be supposed of all, for their forms are mutually exclusive. On *Veronica buxbaumii*, for instance, are many symmetrical flowers, having *two* posterior petals, like those of other Scrophularineæ: these may reasonably be supposed to be ancestral, but if this supposition is made, it cannot be made again for the equally perfect forms with three petals, and the rest[1].

The hypothesis of Reversion to account for the Symmetry and perfection of modern or discontinuous Variation is made through a total misconception of the nature of Symmetry.

There is a famous passage in the *Descent of Man*, in which Darwin argues that the phenomenon of double uterus, from its perfection, must necessarily be a Reversion.

........"In other and rarer cases, two distinct uterine cavities are formed, each having its proper orifice and passage. No such stage is passed through during the ordinary development of the embryo, and it is difficult to believe, though perhaps not impossible, that the two simple, minute, primitive tubes could know how (if such an expression may be used) to grow into two distinct uteri, each with a well-constructed orifice and passage, and each furnished with numerous muscles, nerves, glands and vessels, *if they had not formerly passed through a similar course of* development, as in the case of existing marsupials. No one will pretend that so perfect a structure as the abnormal double uterus in woman could be the result of mere chance. But the principle of reversion, by which long-lost dormant structures are called back into existence, might serve as the guide for the full development of the organ, even after the lapse of an enormous interval of time[2]." *Descent of Man*, vol. I. pp. 123 and 124.

This kind of reasoning has been used by others again and again. It is of course quite inadmissible; for by identical reasoning from the perfect symmetry of double monsters, of the single eye of the Cyclopian monster, and so on, it might be shewn that Man is descended from a primitive double vertebrate, from a one-eyed Cyclops and the like. For other reasons it is likely enough that double uterus was a primitive form; but the perfection and symmetry of the modern variation to this form is neither proof nor indication of such an origin. Such a belief arises from want of knowledge of the facts of Meristic Variation, and is founded on a wrong conception of the nature of symmetry and of the mechanics of Division. The study of Variation shews that it is a common occurrence for a part which stands in the middle line of a bilaterally symmetrical animal, to divide into two parts, each being an optical image of the other: and that conversely, parts which normally are double, standing as optical images of each other on either side of such a middle line may

[1] For a full account of such facts, see a paper by Miss A. BATESON and myself On Variations in Floral Symmetry. *Journ. Linn. Soc.*, XXVIII. p. 386.

[2] This extraordinary passage is scarcely worthy of Darwin's penetration. If read in the original connexion it will seem strange that it should have been allowed to stand. For in a note to these reflexions on Reversion (*Descent*, I. p. 125) Darwin refers to and withdraws his previously expressed view that supernumerary digits and mammæ were to be regarded as reversions. This view had been based on the perfection and symmetry with which these variations reproduce the structure of putative ancestors. It was withdrawn because Gegenbaur had shewn that polydactyle limbs often bear no resemblance to those of possible ancestors, and because extra mammæ may not only occur symmetrically and in places where they are normal in other forms, but also in several quite anomalous situations. In the light of this knowledge it is strange that Darwin should have continued to regard the perfection and symmetry of a variation as evidence that it is a Reversion.

be compounded together in the middle line forming a single, symmetrical organ.

It would probably help the science of Biology if the word 'Reversion' and the ideas which it denotes, were wholly dropped, at all events until Variation has been studied much more fully than it has yet been.

In the light of what we now know of the process of reproduction the phrase is almost meaningless. We suppose that a certain stock gives off a number of individuals which vary about a normal; and that after having given them off, it begins to give off individuals varying about another normal. We want to say that among these it now and then gives off one which approaches the first normal, that shooting at the new mark it now and then hits the old one. But all that we know is that now and then it shoots wide and hits *another* mark, and we assume from this that it would not have hit it if it had not aimed at it in a bygone age. To apply this to any other matter would be absurd. We might as well say that a bubble would not be round if the air in it had not learned the trick of roundness by having been in a bubble before: that if in a bag after pulling out a lot of white balls I find a totally red one, this proves that the bag must have once been full of red balls, or that the white ones must all have been red in the past.

Besides the logical absurdity on which this use of the theory of Reversion rests, the application of it to the facts of Variation breaks down again and again. I have already mentioned some cases of this, but there are many others of a different class. For instance, it will be shewn that the percentage of extra molars in the Anthropoid Apes is almost the highest reached among mammals. On the usual interpretation, such teeth are due to Reversion to an ancestral condition with 4 molars, and on less evidence it has been argued that a form frequently shewing such "Reversion" is older than those which do not. From this reasoning it should follow that the Anthropoids are the most primitive form, at least of monkeys. It is surely time that these brilliant and facile deductions were no more made in the name of science.

3. *Causes of Variation.*

Inquiry into the causes of Variation is as yet, in my judgment, premature.

4. *The Variability of "useless" Structures.*

The often-repeated statement that "useless" parts are especially variable, finds little support in the facts of Variation, except in as far as it is a misrepresentation of another principle. The examples taken to support this statement are commonly organs standing at the end of a Meristic Series of parts, in which there is a progression or increase of size and degree of development, starting from a small terminal member. In such cases, as that of the last rib in Man, and several other animals, the wisdom-teeth of Man, etc., it is quite true that in the terminal member Variation is more noticeable than it is in the other members. This is, I believe, a consequence of the mechanics of Division, and has no connexion with the fact that the functions of such terminal parts are often trifling. Upon this subject something will be said later on, but perhaps a rough illustration may make the meaning more clear at this stage. If a spindle-shaped loaf of bread, such as a "twist," be divided with three cuts taken at equal distances, in such a way that the two end pieces are much shorter than the middle ones, to a child who gets one of the two large middle pieces the contour-curves of the loaf will not matter so much; but to a child who gets one of the small end bits, a very slight alteration in the curves of the loaf will make the difference between a fair-sized bit and almost nothing, a difference which the child will perceive much more readily than the complementary difference in the large pieces will be seen by the others. An error in some measure comparable with this is probably at the bottom of the statement that useless parts are variable, but of course there are many examples, as the pinna of the human ear, which are of a different nature. It is unnecessary to say that for any such case in which a part, apparently useless, is variable, another can be produced in which some capital organ is also variable; and conversely, that for any case of a capital organ which is little subject to Variation can be produced a case of an organ, which though trifling and seemingly "useless," is equally constant. With a knowledge of the facts of Variation, all these trite generalities will be forgotten.

5. *Adaptation.*

In examining cases of Variation, I have not thought it necessary to speculate on the usefulness or harmfulness of the variations described. For reasons given in Section II, such speculation, whether applied to normal structures, or to Variation, is barren and profitless. If any one is curious on these questions of Adaptation, he may easily thus exercise his imagination. In any case of Variation there are a hundred ways in which it may be beneficial, or detrimental. For instance, if the "hairy" variety of the moorhen became established on an island, as many strange varieties have been, I do not doubt that ingenious persons would invite us to see how the hairiness fitted the bird in some special way for life in that island in particular. Their contention would be hard to deny, for on this class of speculation the only limitations are those of the ingenuity of the author. While the only test of utility is the success of the organism, even this does not indicate the utility of one part of the economy, but rather the nett fitness of the whole.

6. *Natural Selection.*

In the view of the phenomena of Variation here outlined, there is nothing which is in any way opposed to the theory of the origin of Species "by means of Natural Selection, or the preservation of favoured races in the struggle for life." But by a full and unwavering belief in the doctrine as originally expressed, we shall in no way be committed to representations of that doctrine made by those who have come after. A very brief study of the facts will suffice to gainsay such statements as, for example, that of Claus, that "it is only *natural selection which accumulates those alterations, so that they become appreciable to us* and constitute a variation which is evident to our senses[1]." For the crude belief that living beings are plastic conglomerates of miscellaneous attributes, and that order of form or Symmetry have been impressed upon this medley by Selection alone; and that by Variation any of these attributes may be subtracted or any other attribute added in indefinite proportion, is a fancy which the Study of Variation does not support.

Here this Introduction must end. As a sketch of a part of the phenomena of Variation, it has no value except in so far as it may lead some to study those phenomena. That the study of Variation is the proper field for the development of biology there can be no doubt. It is scarcely too much to say that the study of Variation bears to the science of Evolution a relation somewhat comparable with that which the study of affinities and reactions bears to the science of chemistry: for we might almost as well seek for the origin of chemical bodies by the comparative study of crystallography, as for the origin of living bodies by a comparative study of normal forms.

[1] *Text-book of Zoology*, Sedgwick and Heathcote's English translation, vol. I. p. 148. In the original the passage runs: "*erst die natürliche Zuchtwahl häuft und verstärkt jene Abweichungen in dem Masse dass sie für uns wahrnehmbar werden* und eine in die Augen fallende Variation bewirken." C. CLAUS, *Lehrb. d. Zool.*, Ed. 2, 1883, p. 127, and *Grundzüge der Zoologie*, 1880, Bd. I. p. 90. The italics are in the original.

PART I.

MERISTIC VARIATION.