Scientific papers of William Bateson

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SCIENTIFIC PAPERS
OF
WILLIAM BATESON

IN TWO VOLUMES

VOLUME I

SCIENTIFIC PAPERS
OF
WILLIAM BATESON

EDITED BY
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VOLUME I

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PREFACE

WHEN the Syndics of the University Press decided to issue a collected edition of Bateson's scientific papers in two volumes and invited me to edit them, it became necessary to decide what should and what should not be included within the limits proposed. For this reason a few remarks seem called for on the scope and plan of the present collection.

It should be at once stated that none of those writings are included in which Bateson appealed to an audience wider than the purely scientific one. These have already been collected and published elsewhere[1]. Apart from them, however, the present volumes bring together practically all Bateson's contributions to scientific journals, with the exception of the papers on the structure and development of *Balanoglossus* published in the *Quarterly Journal of Microscopical Science*, and of the lengthy series of Reports to the Evolution Committee of the Royal Society, 1902–1907. Important as these last are, their omission is less serious in that they are still to be procured from the Royal Society. Fortunately, however, each Report contains a summary of the facts recorded and of their bearing on the progress of genetical science. These summaries are reprinted in the present collection. On the other hand, I have included portions from two of his earlier books which have long been out of print and are difficult to obtain. Of these one is the famous Introduction to the *Materials for the Study of Variation*, and the other, taken from *Mendel's Principles of Heredity—a Defence*, is the earliest reasoned statement of Mendel's work in English.

The arrangement of the papers is on the whole chronological, but I have not hesitated to disturb strict sequence in order to bring together two or more papers relating to the same matter.

As a whole the papers fall into two well-marked groups—an earlier one dealing mainly with problems of Variation, and a later one concerned chiefly with Heredity. Since the two groups are of approximately the same size it has been possible to keep them in separate volumes with little disturbance of chronological order. Each volume will contain its own index, and a full bibliography will be found at the end of the second one. Lastly, with the exception of a few obvious slips or misprints, the papers are as originally published,

[1] *William Bateson, F.R.S., Naturalist, His Essays and Addresses* (Cambridge University Press), 1928.

save for such small textual alterations as were found to have been made by the author in his own copies.

Thanks are due to the following Societies for permission to reprint papers which have appeared in their journals: the Cambridge Philosophical Society; the Entomological Society of London; the Linnean Society of London; the Marine Biological Society of the United Kingdom; the Royal Society; the Royal Horticultural Society, and the Zoological Society of London; also to the Editors and Publishers of *Brain*, *Biometrika*, *The Entomologist's Record*, *Nature* and *The Quarterly Journal of Microscopical Science*.

R. C. PUNNETT

***February* 1928**

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THE ANCESTRY OF THE CHORDATA

[*Quart. Journ. Micr. Sci.* XXVI, 1886]

PREFACE

In view of the facts relating to the structure of the *Enteropneusta* which form the subject of the accompanying paper and of those which have preceded it, it seemed necessary to attempt some analysis of their import and bearing upon morphological problems, and especially upon the vexed question of the ancestry of the Chordata.

But at the outset it was impossible to attempt such an analysis without first clearing the way by a discussion of the morphologic meaning of Segmentation. Since the Enteropneusta are essentially "unsegmented" animals and the Vertebrata are "segmented," this preliminary discussion was necessary. Moreover, having shown reason for not accepting the view that the vertebrate segmentation was of such a kind as to necessitate the existence of a series of segmented ancestors to account for it, it became also necessary to treat the whole question of the origin of segmentations of this class upon a wider basis. This must be the apology for the introduction into this paper of some matter and speculation not otherwise immediately relevant to the subject.

The decision that it would be profitable to analyse the bearing of the new fact in the light of modern methods of morphological criticism, does not in any way prejudge the question as to the possible or even probable error in these methods.

Of late the attempt to arrange genealogical trees involving hypothetical groups has come to be the subject of some ridicule, perhaps deserved. But since this is what modern morphological criticism in great measure aims at doing, it cannot be altogether profitless to follow this method to its logical conclusions.

That the results of such criticism must be highly speculative, and often liable to grave error, is evident.

PART I

The Segmentation of Amphioxus and the Vertebrata, compared with that of the Annelids

From the time when the theory of descent in some form or other became generally accepted amongst zoologists, the question of the pedigree of the Vertebrates has been the subject of much speculation and controversy. The amount of attention which has been bestowed on this question has perhaps been greater than is warranted by the actual importance of the problem considered as a contribution to general biology; but when it is borne in mind that the question is that of the history of the human race, the fascination which has been found in it is not surprising.

Beyond, however, this more sentimental side, there is another source of special interest to be found within the terms of the problem itself; namely, that which is afforded by the obscurity of the solution; for when the relation of any one group to the rest of the animal kingdom is sought, in most cases there are some cardinal features of anatomy common to it and to some other group, which appear to point to some affinity between them. For example, the structure of the Tracheata at once suggests Crustacean affinities, while there is a strong apparent resemblance between the whole Arthropoda and the Annelids. Even a group so isolated as the Mollusca has points of obvious harmony with other groups as soon as the characters of the Trochosphere are known, and similarly with most other groups. Each and all of these "obvious" resemblances may be illusory, but still they furnish something which, temporarily, is satisfying, and at least provides a point of departure for criticism. But in the case of the Chordata there are none of these common features. The three characters which unite them, the notochord, the gill-slits, and the relations of the nervous system, are limiting and exclusive, and without parallel in any forms outside the Chordate group. So strongly has this fact been felt by many of those morphologists who have already dealt with the pedigree of the group, that they have practically abandoned the attempt to find homologies for these features among the Invertebrates; for it is impossible to take seriously such suggestions as, for example, that the notochord may be compared to, generally, the sacs of the Capitellidæ, the "siphons" of any of various Invertebrates, the "giant-fibres" of Earthworms, or the crystalline style of Anodon. Each of these structures has been in turn suggested, together with many others, as offering something with which to compare the notochord. In the same way Semper argues that the vertebrate gill-slits have an obvious similarity to certain pores which he has found in the heads of certain Oligochæta (Nais), while other authors see a striking resemblance between them and the Chætopod segmental organ, and so on.

In seeking, then, for the proximate ancestors of Chordata, the Chordate features have been disregarded, and another character of the vertebrate animal has been selected as offering a more probable basis of operations. The character which has in this way been chosen as the point of departure is that of *metameric segmentation*. By thus setting aside the questions arising out of the notochord, etc., and speculating upon the segmentation of the body, the conclusion is soon reached that some Annelid was the immediate ancestor sought.

This view has found its chief exponents in Dohrn and Semper, and has been generally supported by Haeckel and by most of the popular exponents of evolution.

It would be unprofitable to recapitulate here the numerous morphological difficulties as to the primitive mouth, etc., which arise if this theory be received. Many objections of this kind have been raised and have been variously replied to, and in this condition the matter rests. By those who support it, it is assumed that the common feature of segmentation is so binding and unique a property as to suffice to link together groups whose morphology is otherwise widely different.

In the following pages it is proposed to examine the propriety of employing the character of metameric segmentation as one of first importance in forming a phylogeny of this kind. And before referring to the evidence derived from the fact that the three characteristic features of Chordata are found in Tunicata and Enteropneusta, which are unsegmented forms, it will be best first to discuss the meaning of the phenomenon—"segmentation"—for if resolved into its elements it will be found to be by no means a peculiar feature of a few groups, but rather the full expression of a tendency which is almost universally present.

The term "metameric segmentation" has been used to describe several anatomical features, which reach their highest development in the Annelids, the Arthropods, and the Vertebrata. If an attempt be made to reduce this expression to its simplest terms it appears to mean, in the first place, that certain organs of the body are serially repeated from before backwards, and in the second place that, in the case of the Vertebrates and Annelids at all events, the body cavity is at some period of life divided into a series of compartments, each of which is closed off from its neighbours. But when a more precise account of this phenomenon is required, and when it becomes necessary to particularise as to which of the various organs of the body is thus repeated, difficulty at once arises from the fact that this repetition is irregular, and even within narrow limits may vary considerably. In the case of many of the errant Polychæts all the mesoblastic organs, together with certain apparently serially homologous parts of the nervous and digestive systems, may recur for a seemingly indefinite number of times in one individual, or even the whole animal may be repeated in a chain, thus giving the highest expression to the phenomenon. On the other hand, as in Lumbricus, etc., one or more of the mesoblastic organs may not be repeated; while in both Oligochæts and Polychæts there is a marked tendency to a division of labour between and specialisation of structure of individual segments or even regions of segments in various parts of the body. It thus appears that even among Annelids alone the fact of segmentation is not a circumscribed idea, but may include several phenomena which clearly differ from each other in degree, and possibly are also unlike in kind. For while in the case of Nais, etc., this repetition is complete, and is thus used as an obvious and simple mode of reproduction, yet in other worms it appears only to be concerned in increasing the length of one individual without adding to the number. Now, if these two conditions are merely various expressions of the same phenomenon the question at once arises as to which is its more primitive manifestation. Was segmentation originally a *repetition of all the organs for purposes of reproduction*, which process has become subsequently commuted into mere *increase in bulk*, or is this *complete repetition* to be regarded as the *final term in a series* of which the first was *increase in bulk*? Segmentation, as we know it, may clearly be viewed from either of these two standpoints. With regard to the Annelids, many authors have held that the former is the correct one; the question whether this is so or not cannot be discussed here, but in the case of the Chordata examination will show that their segmentation is of the latter class, and is the result of a summation of repetitions; and, being so, it is by no means a unique condition, which can unite forms otherwise unlike, as Chordata and Annelids, but is rather a result of the common tendency

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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 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

[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 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.

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 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 show 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 *primâ 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 shown 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 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 recognised 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 show 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 recognised 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 realise 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 reflection will show 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 organised 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