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No. VIII

THE SPECIES PROBLEM

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THE SPECIES PROBLEM

AN INTRODUCTION TO THE STUDY OF EVOLUTIONARY DIVERGENCE IN NATURAL POPULATIONS

BY

G. C. ROBSON, M.A.
Assistant Keeper, Department of Zoology, British Museum (Natural History)

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PREFACE

I HAVE attempted in the first part of this work to gather together the records of certain differences between those groups of animals and plants which are rated as species by the systematist, and to consider to what extent the recognition of species is relevant to evolutionary problems. In the second part I have tried to examine as impartially as possible the various theories by which we seek to explain the phenomena of evolutionary divergence as it is manifested in the various assemblages of specific and varietal rank which we can recognise in natural populations of plants and animals.

My only excuse for adding to the already abundant literature on evolution is the belief that I have assembled the data, much of which is already familiar to specialists, in a convenient and synthetic fashion.

The increasing complexity of scientific analysis, the prodigious output of literature and the variety of subjects that may be pressed into the study of evolution render it imperative that some sort of a synthesis should be attempted. I am conscious that the slight sketch here provided cannot be of more use than a summary indication of some of the leading principles involved and of certain types of evidence sometimes neglected in discussions on evolution.

The subject has been treated very largely from the zoological standpoint ; but I have attempted as far as possible to introduce botanical data on the more important issues. I am conscious, however, that there are many omissions, which a fuller acquaintance with botanical literature might have supplied. There are, moreover, several subjects on which I have touched but superficially and with second-hand knowledge. I venture to believe, however, that these deficiencies will not mar the general plan of the work.

The obligations incurred by me in preparing this book are manifold. I have been compelled to consult many specialists in divers branches of our study, and from all of them I have received the fullest and most unstinted measure of assistance. It would be invidious to particularise ; but I must acknowledge the generous assistance of my colleagues of the British Museum (Natural History), and especially the kindly guidance and criticism (perhaps too often neglected) of Mr. C. Tate Regan, F.R.S., and Dr. W. T. Calman, F.R.S. Messrs. J. Ramsbottom, A. J. Wilmott and R. D'O. Good (Department of Botany), Dr. H. A. Baylis, Mr. M. A. C. Hinton and Mr. C. C. A. Monro (Department of Zoology), Messrs. K. G. Blair and N. D. Riley (Department of Entomology), and Dr. W. D. Lang (Department of Geology) have been repeatedly importuned by me and have been more than helpful. I must likewise express my obligation to the late Mr. W. Bateson, F.R.S., whose kindly encouragement and advice are still an inspiration, to Professors E. W. Macbride, F.R.S., and A. E. Boycott, F.R.S., Dr. J. C. Ledingham, F.R.S., Mr. C. C. Dobell, F.R.S., Professors D. M. S. Watson, F.R.S., J. S. Huxley and R. R. Gates, Captain C. Diver, and Messrs. C. S. Elton and O. W. Richards. I am particularly indebted to Mr. Richards for his assistance and co-operation. Any errors of fact or judgement that may occur in this work on matters concerning which these gentlemen are special authorities, are to be attributed to myself alone and not to them, as they are not responsible for the matter actually set down herein.

G. C. ROBSON.

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CHAPTER I

INTRODUCTION

IT is generally conceded at the present time that, while many of the groups called " species " by the systematist are readily distinguishable one from another, there is no universal criterion by which species as opposed to other systematic units may be recognised. The grounds on which this conclusion rests will be set forth in detail in the body of this chapter. It is enough to say at present that the groups treated as species by the systematist are variously differentiated in the number and the distinctness of their peculiar characters, and that the various criteria of distinctness, though in a broad sense they march together, are often mutually contradictory and do not allow us to formulate a standardised method of diagnosis.

For this reason I have passed somewhat lightly over the old contentious discussions as to the nature of species, and have regarded the species problem very largely as the problem of evolutionary divergence. I retain the title of this work rather out of courtesy to a time-honoured and useful convention than from the belief that the initial stages of divergence are better studied in the form of taxonomic species. At the present time there are signs in evolutionary studies of a renewed interest in the study of variation and race-formation in relation to habitat and mode of life. Herein the species is of less importance than the " race " or the colony. Nevertheless, as stated more fully elsewhere, the amount of information concerning the vital affairs of plants and animals that is attached to species is far more abundant than that which is available for varieties, races and colonies. We are thus compelled by the present arrangement of our material to have more frequent recourse to the species as a point of reference. A summary of the various modes of divergence—physiological, structural, ecological, etc.—as they are recorded in relation to species, seems desirable, and is here presented with due consideration of varietal and racial differentiation.

In Darwin's own words, " species come to be tolerably well-defined objects " (1859, p. 213), and, as such, their attributes are deserving of attention, always provided that we steadily bear in mind that they are not equally homogeneous, and that sometimes specific rank is accorded to individuals which are not known to be representatives of naturally " well-defined " populations.

Even at the present time, when there is some measure of agreement as to the nature of species, we still find the question regarded from very different standpoints. We find E. Rabaud (1920, pp. 291-3) declaring that the individual is of greater consequence than the species, while Bateson (1913, p. 12) is of the opinion that " specificity " is a universal attribute of organised life. Most zoologists and botanists are by now probably convinced that the truth lies midway between these extreme opinions, and that, while there is no essential and absolute " specificity " which can be attributed to certain assemblages of individuals, but not to others, the groups which the systematist treats as species have a tolerable degree of homogeneity. The systematic status of such groups is generally recognised as a purely conventional matter. As a preliminary, however, we ought to examine this opinion carefully. Our ideas concerning the process of evolution have been coloured in the past by our estimate of the species-concept, and we ought to attempt to form as clear and well-founded a view as possible on the latter before discussing the process of evolutionary divergence.

An account of the history of the species-concept has been given by Bachmann (1905), and Bateson (1913) has supplied a critical study of the modifications of the concept since Ray's *Historia Plantarum* (1686). It is unnecessary to discuss the various views and definitions which have been put forward by distinguished naturalists. " Tot sententiae quot homines " is an aphorism which has particular application to the definition of species. From Linnæus onwards the definitions are copious. The majority of the earlier definitions are more concerned with the species as a whole, and the sum total of resemblances or differences between species, than with the *degree* of resemblance or difference between them or the extent to which different parts of the organism are affected by differentiation. Thus Cuvier (1829) asserted that the species is " la réunion des individus descendus l'un de l'autre ou de parents communs, et de ceux qui leur ressemblent autant qu'ils se ressemblent entre eux ", though he goes on to introduce a note of doubt concerning his definition—" on sent que son application à des individus déterminés peut être très difficile " (*l.c.* p. 17). The definition of de Blainville (quoted in Godron, 1872, p. 5)—" l'espèce est un type d'organisation *de forme et d'activite plus ou moins déterminé* qui se perpétue dans le temps et l'espace par la génération "—contains a suggestion of uncertainty and an extension of the criterion from the purely morphological basis. L. Agassiz carried the inquiry deeper, in that he was concerned with the mode of distinction, and rightly saw that " les éléments de structure des organismes ne sont pas de valeur égal ". A distinct advance was made by Godron (*l.c.*) in the clear recognition of other criteria than the morphological. But his verdict, " c'est un fait incontestable que *toutes* les espèces animales et végétables se séparent les unes des autres par de caractères absolues et tranchées " (vol. 2, p. 372), is one which is not likely to be acceptable at the present time. The analysis of the problem was carried forward considerably by A. Jordan's recognition of " elementary species " and his demonstration of the polymorphic nature of the Linnæan species. The way was thus prepared for de Vries' statement of the problem and his special theory of the discontinuous origin of species, which involved a consideration of the nature of fluctuating variability. The contributions of the Genetic school to the problem are more fully discussed anon, though we must mention the critical discussion as to the harmonising of the various concepts of specific difference in which Bateson (*l.c.* p. 234 and following) defined the scope of future genetic inquiry in this field. Of recent years many experimentalists have admitted and stressed the discrepancy often noted between morphological and genetic criteria (cf. Babcock and Clausen, 1918; Shull, 1923; and Guyénot, 1924) and the absence of a universal criterion of " specificity ".

We have so far been discussing a concept of species which involves an acceptance of the idea that they are invariably determinate entities having well-defined properties. Needless to say this doctrine is in sharp contrast to that which is implied in the theory of Natural Selection. Darwin regarded the term " as one arbitrarily given " (*Origin of Species*, p. 66), and laid it down that " no clear line has as yet been drawn between species and varieties ". To make the latter distinction he fell back on " the opinions of naturalists having sound judgement and wide experience " (*l.c.* p. 57). Sometimes the difference between species is plainly perceptible, the discrimination of " doubtful " species being purely a matter of systematic convention. Those who accept his views consider that the distinctness of species or of varieties is due to the extinction of ill-adapted forms and to divers modes of isolation (ecological, sexual and topographical), that the degree of distinctness is extremely varied and entirely dependent on the number of structures which are, either directly or indirectly, brought under the influence of adaptation by selection. However much difference of opinion there may be as to the causes of variation, I believe that Darwin's concept of species represents the opinion of the majority of biologists to-day.

The growth of comparative physiology was accompanied by a realisation of the more intimate effects of " specificity ". We owe to Przibram (1910) an attempt to reduce the various criteria to a systematic order, while a valuable summary of work on biochemical differentiation is given by Schepotieff (1913).

Of contemporary authors tribute must also be paid to the attempt of Lotsy (1916) to give a fresh orientation to our analysis of plant and animal relationship by means of a new terminology. Attention should be drawn to the attempts of Davenport and Blainkinship (1898) and others to provide a graphical method of expressing specific differentiation. Such devices, though of considerable value as setting forth the varying degrees of differentiation between allied species, have not been very vigorously followed up. While admitting that the graphical method recommended by these authors is purely conventional, we cannot but think that, if some such method were adopted at large by taxonomists, we would obtain a better insight into the facts of correlation and character-grouping than is provided by the present technique. The attention of the taxonomist, as well as of the general student, is likewise drawn to the suggestions of Lutz (1908), Vavilov (1922), and Pilsbry, Hyatt and Cook (1912), that some method of formularising the various stable character-combinations is of service.

Finally, we must not omit reference to those intensive studies of individual species which were initiated by Jordan in his investigations of *Draba*. Amongst zoological studies of this nature the pioneer work of Coutagne (1895) is to be mentioned, as well as the intensive regional surveys of Birds and Mammals that have supplied valuable data on geographical " polymorphism ".

Every living organism exhibits a large number of attributes to which we give the name " characters ". Such " characters " include every structure and property of the animal or plant, whether they be organs, cytological structure, physiological activities, habits or ecological relationships. It is often objected that to regard the living organism as a bundle of separate " characters " is an unphilosophical method, and that to dissociate and describe separately the individual characters is to do violence to the inherent unity of the organism. Developmental physiology has taught us something about the " organism as a whole ", the correlation and mutual dependence of the individual parts. But evolutionary biology is largely a matter of analysis and description, and while, as we shall see later, the question of correlation is of great importance, we would be exaggerating the concept of the " organism as a whole " if we insisted that the individual parts considered separately have no significance. It is likewise waste of time to insist that an organ such as a leaf or the radula of a snail is the resultant of a large number of cytological activities, and that for this reason the radula or the leaf should not be isolated from their cellular components. We may well believe that specific divergence is to be found in the cytoplasm of the cells of which any organism is built up. But an organ such as the radula of a snail is the finished product of certain local activities ; and, as such, it can be regarded apart from the rest of the organism without doing violence to the more profound unity of the latter.

If we examine any of the definitions of species which have been put forward, we shall see that there is implicit therein the idea of a criterion. Certain individual organisms are to be grouped together because they resemble each other in certain respects. The latter have never been comprehensively defined ; and it will be seen that such definition is impossible. The basis of resemblance can be any of the countless attributes that we distinguish as " characters ". It may be any part or parts of the structure, the physiological activities, the habits, food, distribution—in short, any of the ways in which an organism impresses itself on our notice.

The first and most obvious query which we should make, in examining the criterion of specific status, is whether the species-concept is valid within any one particular group of attributes, *e.g.* structure or physiological activities. We should also inquire whether differentiation is manifested in all the attributes regarded collectively.

Morphological Criterion

The zoologist recognises two forms of *Lepus* which live in the British Isles at the present time, *Lepus timidus*, the Mountain or Varying Hare, and *Lepus hibernicus*, the Irish Hare. They are distinguished one from the other by many structural features (coat-colour, skull, dentition and size). On the other hand, they resemble each other sufficiently for them to have been regarded by some naturalists as varieties of the same species. Beyond purely arbitrary tests we have no means by which to decide the exact measure of their relationship. None of the many differences which we might describe are recognisable in themselves as an index of specific or varietal status. In practice we describe a limited number of characters, and close our definition at an arbitrary point. But, if we described the whole set of attributes of each, we would be still devoid of a universally applicable standard by which to assess the differences as varietal or specific. Moreover, it must be recalled that, though some measure of distinctness in certain characters may impress itself on our attention if we examine a certain number of these animals, the impression thus formed is dependent on the number of specimens examined. Possibly those specimens may be a " true " sample, *i.e.* on analysis they are found to represent the average constitution of a larger population. But very often the number is limited, and we have no means of judging how far it is representative of the natural population past and present. This consideration may seem to involve taxonomic practice rather than the question whether there is a standardised species or variety. But it must be borne in mind that the concept of species has largely arisen out of taxonomic experience, and that the latter can rarely be based on a survey of the entire population from which its samples are drawn.

The attribute of " discontinuity " or " distinctness " has always lingered around the concept of the species. " Discontinuity ", as we shall see anon (Chap. VII.), is a crude concept, and difficult to apply to the relationship of living organisms as expressed in their structure, habits, etc. It is true that a difference in a structure having meristic expression may be discontinuous, *i.e.* there may be an appreciable difference between ten and eleven appendages of a Polychaet worm, or between four and five coccygeal vertebræ in Man. But, as Bateson (1894, p. 18) admitted, " it will not be possible to find any general expression which shall accurately differentiate between variations which are Discontinuous and those which are Continuous ". In any case it is extremely difficult to apply the notion of discontinuity to sections of natural populations which may be differentiated in any number of characters.

The Irish and Mountain Hares are distinguished from each other by a number of well-differentiated characters. But when we examine any group of organisms which have been subjected to systematic analysis, it becomes obvious that the number of characters in which differentiation is established is exceedingly variable. This fact is so widely recognised that it is unnecessary to give examples. Moreover, in addition to variation in the number of differentiated characters, we encounter great variety in the degree of distinctness of individual characters. Thus two species may be separated by differences in, *e.g.*, five characters. But of these five two may be very distinct in the two species, the remainder less distinct, though still " discontinuous ". Again, another pair of species may be differentiated in respect of a number of characters of which some may be distinct while the others grade from one into the other. The subject of *intermediacy* will be more fully dealt with in Chapters II. and VII.; but it is necessary to consider it briefly at this point. Bateson (1909, p. 236, and 1913, p. 131) has shown that intermediacy may be due to various causes which may actually mask genotypic distinctness. Thus intermediates may be found between two species which are of a fluctuational nature, and therefore devoid of hereditary significance. Or again they may represent a heterozygous condition. Nevertheless, though it may be possible to show that two forms are genotypically distinct in spite of the presence of intermediates between them, the revelation of such distinctness does not help us to the recognition of species. " Discontinuity " may be expressed in one character or in many, and, as far as an absolute criterion of species is concerned, we cannot, except on a purely arbitrary basis, specify how many character-differences must be involved. The question as to whether species are " real " or " arbitrary " is often confused with the question of their " distinctness ". The taxonomist may distinguish the extremes of a continuously graded series of forms as species, or he may recognise forms as distinct which may differ in any number of discontinuous characters. Now we may succeed in showing that in the first case actual discontinuity is masked by hybridisation or plastic responses to environmental stimuli. But neither this nor any sort of discontinuity is an index of " specificity " in the sense in which it is usually employed, unless at the same time we can show that there is a standard discontinuity in the number of characters differentiated in a species on the one hand and a variety on the other. Of this we have no evidence. Proof of discontinuity is then no index of " specific " status.

It is thus apparent that as far as the structure of living animals and plants is concerned we can draw no hard and fast line between species and variety, and can formulate no absolute criterion of the former. We are in fact dealing with a tendency to differentiation which is expressed in manifold degrees.

Of course if we can point out, as we undoubtedly can among living forms, character-groups admittedly of varying magnitude which seem to possess a certain distinctness and obvious individuality, it might seem sufficient. Species would then be of admittedly diverse composition, but of definite individuality. The composition of the groups which are recognisable in natural populations will be discussed in Chapters II. and VII. We are at present, however, concerned with the degree of differentiation of animal and plant structure, and whether the latter is divisible into discrete units having standardised attributes.

To sum up, it is apparent that at the morphological level no rigid definition of the species is obtainable. There is every degree of differentiation in the number of characters affected, and we can apply no absolute criterion. That a great number of forms do attain a certain status of differentiation and maintain that status for long periods is certain. But we have no evidence that enables us to standardise a particular degree of differentiation as " specific ".

Genetic Criterion

When the work of Mendel was republished in 1900 and the study of heredity acquired an experimental technique, the former became, not only a method of impartial research, but also an instrument of evolutionary inquiry largely employed as a basis for the criticism of the doctrine of Natural Selection. Even before the date in question, de Vries had found in the discontinuity of his *Oenothera* mutants a basis for attack, and Bateson (1894) had systematically arranged certain phenomena of variation with a similar end in view. Discontinuity of the characters of species originating by " mutation " and maintained as units by segregation thus became a weapon of controversy, the species recovered something of its former prestige, and " specificity ", or the essential property of species, became an object of inquiry. I cannot help thinking that the species was thus restored to prominence under the mistaken notion that the established and undeniable fact of the discontinuity of unit characters involved also some standard discontinuity between the groups of such characters recognised as species by the systematist. However that may be, the general result of genetical research has falsified the hopes of those days. The criticisms of Natural Selection founded on genetical inquiry have been a substantial and valuable contribution to the study of evolution, the relationships of groups recognised as species have been intensively studied, and the nature of intermediates has been elucidated; but it cannot be said that the universal property of " specificity " has been hereby established.

One of the main ideas of the early workers in Mendelian analysis was that genetical study would supply a criterion by which species would be distinguishable as such. An attempt was made by de Vries (1903) to make a distinction between species and varieties based on the occurrence of segregation in crosses between the latter and its absence in species-crosses. We owe to A. Lang the aphorism "Arten pendeln, Varietäten mendeln", a concise statement of that position. This generalisation was criticised by Bateson (1909, p. 285), though the latter expressed the opinion that genetic research might ultimately provide some approach to a valid distinction between species and variety.

The de Vries-Lang proposition was founded on an inadequate realisation of the disharmony sometimes found between the various criteria of species as well as upon a misconception as to the nature of the characters that seem to exhibit blending. The distinction between characters which behave as simple segregates and those which do not usually depends on the number of factors involved, and not on a fundamental distinction into segregating and non-segregating characters.

There is no immediate correlation between morphological status and the complexity or simplicity of factorial composition. There is plenty of evidence that individual characters in "varietal" crosses behave in a fashion which departs just as much from simple Mendelian ratios as those of "specific" crosses (*e.g.* East, *Nicotiana*, 1916; Setchell, Goodspeed and Clausen, 1922, pp. 469 and 505). Simple segregation has been recorded in crosses between distinct morphological species by Rasmuson (1921), Surface (1916), Wichler (1913), East (1916 B), and others.

I do not feel that we can say with certainty that simple segregation is not to be attached to any particular morphological status or degree of affinity, but is entirely a question of factorial composition. If, however, we admit that the readiness or the difficulty with which segregation can be shown to be operative is dependent on the number of factors involved, we are not thereby relieved of the necessity of explaining how it is that some characters are dependent on few factors and others on many. Nevertheless, there is little evidence available which might suggest that degree of relationship contributes to differences of this kind. It is true that Harrison (1920 B) has shown clearly that melanism exhibits simple segregation in an intraspecific cross, while in an interspecific cross it behaves in a very different fashion. Rasmuson (1921), however, obtained no difference in the simplicity or complexity of segregation in varietal and specific crosses of *Godetia*.

The question, therefore, of factorial composition does not seem to me to have any direct bearing on the status of species as determined by morphological criteria.

In discussing the continuity or the discontinuity of species, whether at the factorial or the morphological level, we must carefully distinguish between the discontinuity of single characters and the discontinuity of character-groups. Of the former we have ample evidence; but the question left unanswered by de Vries and his followers is—to what sort of such discontinuous characters are we to assign specific status, and to what number?

Experimentalists have for a long time now rejected the idea originally put forward by Huxley that the inability to obtain fertile offspring on crossing is a sure index of specificity. It is a fact of common knowledge that there is every possible gradation in the reproductive capacity of morphologically differentiated species from absolute fertility to complete sterility. At the very offset we have the phenomenon of self-sterility to refute such a criterion (Darwin). It is worth our while, however, to assemble some of the typical stages in this gradational series. At one time or another the following results have been recorded:

(1) Positive hostility between the male and the female.
(2) Absence of hostility; inability / disinclination } to pair.
(3) Coitus without reproduction.
(4) F_1 obtained but with disturbed sex-ratio, ill-health or other abnormality.

(5) F_1 normal and healthy, but sterile.
(6) F_2 obtained, but weak or unhealthy.
(7) Fertile and viable F_2.

We should next observe that in certain cases differences in fertility between morphological "species" are to be found in reciprocal crosses. Thus Newman (1915) found considerable differences in the viability of Teleost hybrids in such circumstances. The same author (*l.c.*) found that ordinal crosses were sometimes more successful than family or generic ones!

We may finally point out that Harrison (1917) finds that the hybrids obtained by crossing certain Bistonine moths are fertile in spite of marked morphological differences between the parent species (cf. *Poecilopsis pomonaria* and *isabellæ*, p. 280); while conversely Bonnier (1924) and Sturtevant (1920) show that *Drosophila melanogaster* and *simulans*, though differing in only very slight structural details, give infertile hybrids. Harrison (*l.c.* p. 310) also shows that *Poecilopsis isabellæ* and *lapponaria* are completely sterile, in spite of the fact that for many years they have been regarded as conspecific. Nevertheless, we must admit that there is a general parallelism between structural and physiological differentiation.

In the light of this evidence we might urge that there is a point at which a definite line can be drawn, viz. the fertility of the hybrids. This remains, however, no less an arbitrary criterion when we consider the differences in viability that have been observed among F_2 offspring from species-crosses.

On the whole, then, we must agree that the breeding test does not give us a universal criterion, and that it is a regular and consistent index of morphological differentiation only in a very wide sense.

Physiological Criterion

Our knowledge of the degree to which animals and plants are differentiated in respect to their physiological properties into groups coextensive with morphological groups is as yet very imperfect. This field of research is discussed in detail in Chapter III. It will be seen therein that individual, sexual and seasonal idiosyncrasy must be evaluated with particular care in dealing with alleged " specific " divergence in this respect. We have some evidence of group-differentiation in sundry physiological and biochemical activities. But, as far as concerns any parallelism between physiological differentiation and structural and other differentia, we encounter precisely the same difficulties as we have outlined in the preceding sections. Barcroft and his fellow-workers (1924) have pointed out that the spectroscopic examination of the blood of various animals shows that there is no parallelism between morphological status and hæmoglobin characters. Closely allied taxonomic species sometimes exhibit profound differences in this respect. For example, the mollusc *Planorbis albus* has colourless blood and *P. corneus* red blood. Reichert and Brown (1909) have shown that the crystallographical properties of vertebrate hæmoglobin show some parallelism to morphological status. But we note that, according to their results, the Dingo is further removed from the Common Dog than is the Silver Fox (*Urocyon*) in this respect. Similar anomalies are seen in the cases of *Lynx* and *Felis*. Apart from the actual parallelism between physiological and morphological attributes, we find in such of the former as have been studied from this point of view the same diversity in differentiation as makes it difficult to recognise morphological " species ". The work of Reichert (1919) on the starches of plants makes it plain that, when a number of physical and chemical characters are studied, the same diversity of combinations is found as that which makes specific distinction difficult to define from the structural characters (cf. *l.c. Crinum*, Chart E 7 and 8, p. 266).

Ecological Criterion

We are at liberty, if we wish to adopt such a procedure, to regard every form which occupies a distinct habitat as a distinct unit. Some agreement with the physiological criterion might be contemplated herein, for it is likely that difference of habitat may be sometimes the cause or the effect of physiological differentiation even among individuals of the same morphological species. Nevertheless habitats are as difficult to define rigorously as are species. Moreover, this procedure would commit us to regarding as identical all the forms which occupied, *e.g.*, a single habitat, such as a pond or a hedge-bank, so that a crude disharmony between the morphological and bionomic criteria arises.

The only conclusion at which we can arrive is that there is no criterion by which we can define and delimit separate units of the status required by the species-concept. There may be a general sense in which the four criteria we have discussed are simultaneously applicable. But the degree to which in any one instance differentiation is manifested in respect of these is so variable that it defies organisation in the sense required by the concept. It is not only impossible to find a standardised type of group by applying any single criterion; but also the various main criteria do not give the same results, the same indications of affinity.

We have been at some pains to show that there is no universal criterion of species, and that the groups so designated in systematic zoology and botany cannot be regarded as a category having attributes which distinguish it from other categories. Such groups, however, can be profitably discussed when we know that they are composed of a large number of individuals having certain characters in common. We may find on analysis that such groups can be resolved into secondary groups, into elementary species or local races; we may find it quite impossible to decide what status we ought to assign to a particular assemblage, and the groups we designate as species may turn out to be mere abstractions from a *continuum* of imperfectly correlated character-lineages. But on the whole we find that both in time and in space the natural assemblages or population of animals tend to form groups of individuals resembling each other more than they resemble the individuals of other groups.

But if we can discover no universal criterion of specific status and regard it as a purely systematic convention indicative of groups of diverse constitution and size, in what sense can we speak of a " species problem " or discuss the attributes of species ? If as groups they have no universal properties, how can we profitably discuss them ? We have to admit that there can be no " species problem " in the sense of a discussion of the attributes of an entity having fixed boundaries and definite properties. But there is a species problem in the sense that the various groups recognised as species by the systematist, having different degrees of relationship and differing from each other in divers attributes, represent episodes in evolution. In considering the attributes of species on their own individual merits and in respect of the various ways in which divergence takes place—in structure, physiological activities, distribution — we are adopting the normal method of evolutionary inquiry. The only differences of method involved in the treatment of the subject in this work are (1) that we shall attempt to ascertain how far divergence in physiological, structural and distributional attributes go hand in hand, and (2) that in attempting to discuss the origin of divergent groups we shall lay stress on the correlation of divergent characters within natural populations of plants and animals.

Two objections may be lodged against this procedure, of which one is indeed at first sight a valid criticism of all discussions of evolution that employ the species as a unit.

(1) It may be argued that systematic species are often founded on very inadequate information and material, and that in arguing from the difference between species we run the risk of making assertions as to evolutionary divergence that are really not of value, because our premisses are uncertain.

Let us illustrate this objection, by no means an unimportant one, by reference to the two river-crayfishes, *Cambarus virilis* and *Cambarus immunis*, alluded to on

p. 93. We may ask the question—of what advantage is it to discuss and describe differences of habitat attributed to two species, the constitution of which is only known from localised samples of a larger population of quite unknown composition? May not the population, from which the systematist has abstracted a certain number of individuals for description, have such a diverse structural and physiological constitution, that the attribution of certain differences to a limited number of individuals is relatively unimportant? Any species so described, however, is a sample of part of a population, and, even if we may exaggerate its distinctness by treating it as a systematic unit, its attributes are of evolutionary consequence. In special cases, however, the amount of importance we are to attribute to specific status is of some moment, and to these allusion is made in the proper place.

Though we may grant that the peculiarities attributed to species may have at least a partial significance, especially if an intensive regional survey informs us that a species is more or less homogeneous, there is another general criticism to deal with. We may feel after all that the important question in evolutionary science is how any single hereditary difference arises, and by what means it may become a characteristic of a large population. The groups, whether we call them species, or varieties, or races, which differ from each other in respect of several such characters either continuously connected by intermediates or discontinuous, may seem of little significance as such. If we regard species simply as groups (discontinuous or continuous as the case may be) without reference to the individual characters which distinguish them, I grant that this criticism is well founded. But, as it is by some measure of correlation of the differentiated characters that the systematist often recognises his species, we are bound to consider not only the separate characters, but also the reason for their association. Thus, if we find a group of animals recognised from all other groups by the possession of characters A, B, C and D, we are compelled to account for the collective relationship of these characters, which involves a consideration of the species. The latter may be a complex made up of single characters, and continuity or discontinuity between the characters of related species may be entirely dependent on the accidents of extinction or isolation; but at the last resort only a study of the group of characters as a whole can authorise us to speak as to the effects of extinction or isolation.

(2) The significance attached to "colonies", local races, etc., may incline us to believe that the divergences between allied races are of more importance than those between species. In any case, it may be felt that we ought not to confine our attention to specific divergence alone.

In practice, however, it is obvious that species have become, for reasons of convenience and by the development of biological technique, the reference point at which the great bulk of information concerning the divergence of organic beings is assembled. The greater part of our knowledge concerning all save the superficial characters of animals and plants is assembled around the taxonomic species. The anatomy of races, varieties, and the members of colonies and communities, is scarcely ever investigated, although it is seriously in need of such study. The habits, exact distribution, reactions, etc., of such groups are not often recorded, though several intensive studies of the distribution of local races have been made. The genetical analysis of varieties has been frequently conducted with plants, less frequently with animals, while of the physiological differences of varieties and races practically nothing is recorded. It seems then that, willy-nilly, we must deal chiefly with species; though, where it is possible, we will draw on the facts recorded concerning races and similar categories.

The second, third, fourth and fifth chapters will deal with special aspects of specific divergence. The second part of this work will contain a discussion of the mode of evolutionary divergence, as it relates to species. The latter involves the study of two distinct tendencies, viz. the origin of any single variant character and the correlation between such divergent characters which makes it possible to recognise species and similar groups. My object will be to ascertain if the correlation known to occur between divergent characters represents the coincidence of separate episodes of direct transformation by the environment, selective adaptation, or " mutation ", or whether other principles of correlation are involved.

The proposal is frequently made that the concept of species and the systematic method of specific diagnosis should be given up in favour of some other system preferably based upon some recognition of the method in which the differentiated characters are variously combined. The rejection of the systematist's concept does not, however, seem to be implied in these conclusions. Ill-defined as they may be and of varying dimensions, a certain tendency to character-groupings of a certain stability is fairly recognisable, and such grouping requires designation, the only difficulty being the line to be drawn between " species " and " variety ". From the point of view of classification, it seems more desirable to retain that admittedly arbitrary device than to adopt a system of elaborate symbolic representation. At the same time there is no doubt that, if the systematist were to adopt some method of expressing character-groupings and combinations as an adjunct to his traditional method, it would illustrate the structural relationships of allied forms in a very useful manner.

CHAPTER II

THE CONSTITUTION OF SPECIES AND NATURAL POPULATIONS

IN the preceding chapter I dealt with the species-concept and the criteria of " specificity ", upholding the view that there can be no absolute criterion by which species as standardised classificatory units can be always recognised. Nevertheless, as we are continually reminded that well-defined groups do occur, of which individual representatives having the same structural constitution may be found in places distant from each other and after long intervals of time, and as we are anxious to learn something of the means whereby such groups become established, their constitution and their various attributes are desirable objects of study. As a preliminary, however, we ought to inquire how far the groups of admittedly different constitution designated as species are homogeneous, and what relation they bear to the natural populations of animals and plants from which they are abstracted. I open a book on general biology and I find certain habits and reactions attributed to individuals of the Crustacean *Asellus aquaticus* found near Paris. Now we may ask—to what extent are we entitled to think that there is a group of individual animals always recognisable in virtue of certain features as *A. aquaticus*, and to what extent may we postulate of the "*A. aquaticus*" reported from Wastwater, in Cumberland, the various attributes of the French form ?

The matter now to be discussed relates to the structure of animals and plants. Whatever other basis of distinction there may be available, our description of evolutionary phenomena and our classification is essentially morphological, and, until we have produced a synthesis of all the modes of divergence, we must largely be bound by structural features as a clue to affinity.

It is not at present easy to decide how and under what influences the cellular activities responsible for forming a given structure, for example, the shell of a snail or the ribs of a leaf, produce the differences which such structures exhibit in allied species. When quantitative differences between individuals or populations are known to be dependent on the amount of nutrition or tissue-building substances available in the food or the medium, it is easy to see how excess or defect in the supply of food, etc., is translated into structural differences. Nor is there any difficulty in explaining somatic differences in colour that are produced by certain crude environmental factors. Differences in proportion, shape, surface-sculpture and pattern, as well as colour-differences not demonstrably dependent on the availability of formative material are, however, less easy to explain. We know, of course, that the mineral and organic substance of a snail's shell is laid down in a certain fashion, and that the activities of the formative cells are differentiated so that some of them lay down more mineral substance than others. We know that alternating periods of rapid and slow growth may give rise to certain gross differences in sculpture. But we do not know what is the nature of the cytoplasmic differences of the various cell-masses on which specific differences in secretory activity are founded. Some progress has indeed been made, for example in the investigation of colour-production. Studies like those of Wheldale (1907) on the anthocyanin of the Snapdragon enable us to recognise the chemical activities that give rise to various differences in colour. Miss Wheldale showed that the "ivory" forms of *Antirrhinum majus* contain a glucoside absent from the white flowers. We are here, however, in presence of the end-product of cellular activity, and obtain no clue to the cytoplasmic differences which determine the original acquisition or loss of the glucoside.

It therefore follows that, while we can speak of physiological, chemical and physical differentiation in a general way, and while we may believe that it underlies and precedes structural divergence, we are very often in the dark as to the exact steps by which it expresses itself. The various kinds of physiological and chemical differences that we shall see (Chapter III.) in the proteids for example, in various differences of metabolism, in immunity, etc., cannot be directly recognised as *causes* of structural diversity. It is conceivable indeed that they are often effects of the latter. We are therefore bound to consider structural differences as objects of study in themselves, and apart from their chemical and physical antecedents; and in this chapter I shall consider certain general problems illustrated by structural divergence.

There is a surprising lack of data on the total resemblances or differences of related species of animals. The systematist usually indicates a limited number of characters sufficient in his opinion to distinguish his species, and very seldom pursues his inquiry into the total structural organisation. The morphologist, on the other hand, while he frequently gives detailed accounts of the complete organisation, very rarely troubles to deal with more than a single species of a genus. The result is that there are available few reviews of the total organisation of all the species of a genus, so that it is frequently impossible to state whether a certain organ-system is, or is not, differentiated. Again, in trying to draw any general conclusions from our results we have to bear in mind that the systematic technique is not the same for all groups. In certain classes and orders of animals there has been a tradition of anatomical investigation which has worked hand in hand with the citation of external differences. In other cases this has been absent. In the Pulmonate Gastropoda, for example, such a tradition has for a long time supplemented the results of the conchologist. In the Cephalopoda, on the other hand, but little is known of the internal structure of the many hundreds of described species. The same seems likewise to be true of the Lepidoptera on the one hand, in which the genitalia have been studied for many years, and of the Coleoptera on the other, in which that system has not been so well explored. Very probably this system has not often the same systematic value in the Coleoptera as it has in the Lepidoptera ; but for a decisive verdict on its value we require a far greater amount of data on the Coleoptera than is now available.

Subject to these obvious limitations and the conditions which sometimes of necessity render the systematist's task a highly artificial one, namely, the poverty or inadequate preservation of his material, let us return to our principal theme. When the systematist has plentiful material at his disposal, what are the circumstances in which the recognition of discrete groups is possible or impossible ?

A

I. Diverse Composition of Natural Populations : Intermediacy

In Chapter I. I stated that taxonomic species are found to be distinguished from their near allies by a number of characters and a measure of distinctness of the latter, which vary from case to case. If we examine any natural population or the populations representing two closely allied forms, we do not as a rule find perfectly homogeneous associations of characters. We find more usually that the individuals constituting such aggregates are divisible into subordinate groups, and that at the periphery of the area of distribution they may grade into other similar groups. The characters borne by the individuals constituting such populations are sometimes combined in such a way that each individual character may figure in several combinations in a varying degree of frequency. In such populations there is no very high measure of correlation, and the characters are largely interchangeable.

The species which we habitually deal with in Zoology and Botany are essentially systematic creations, and there can be little doubt that we habitually denominate as species groups of diverse constitution, *e.g.* compact homogeneous groups and others of composite nature containing very diverse genotypic elements. Though there may be species which are largely systematic fictions, *e.g.* described as such from a single example, there are forms which in time and space exhibit a large measure of individuality and homogeneity, and can be regularly recognised from their near allies. But exactly how homogeneous they are, to what extent the same characters are found in association over the whole area of dispersal, and how sharply they are demarcated from other forms at every point in their range, is very uncertain. Our knowledge rests on small samples collected here and there, and very rarely do we know the constitution of the whole array of individuals designated as a species. If, then, we wish to know how far any group described as a species, or as a variety[1] or race, is homogeneous, and to measure thereby the effects of the forces making for divergence and multiplication, we should confine our attention to those massive studies of variation, the technique of which was first employed by A. Jordan (studies on *Draba*).

That the Linnæan species were often collections of diverse elements was recognised by Linné himself, and subsequently by de Candolle (cf. de Vries, 1909, p. 166). Jordan and Rosen applied a practical analysis in the use of which they have been followed by many botanists (de Vries, Almquist, Shull) and agriculturists. The study of natural populations of animals has been made by Coutagne (Mollusca), Duncker, Heincke, Schmidt and Regan (Fish), Gulick and Crampton (Mollusca), Lutz (*Gryllus* and *Melipone*), Tower (*Leptinotarsa*), and Lloyd (*Rattus*). Less intensive regional surveys have been made by Allen (Woodpeckers), Swarth (Fox-sparrows) and others. Perhaps it is as well to point out that an intensive study of a large number of individuals from a small area, and the study of samples of the whole population constituting a species collected from different points, necessarily constitute different operations and yield answers to different questions.

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[1] The term "subspecies" is often used instead of "variety" to denote well-marked subdivisions of species.

The essential results of these studies seem to be as follows:

(1) Forms which are given specific rank and are distinguished in several characters from allied species are often composed of subsidiary groups which may occur as geographically distinct races or as separate hereditary strains, the individuals representing which very often live together and interbreed, but are capable of being bred-out into distinct stocks (biotypes).

(2) The aggregates of individuals forming local races, biotypes or larger composite groups are sometimes sharply distinguished one from another, or else they may "intergrade". The individuals of intermediate appearance, either as "mid-intermediates" or as combinations of the characters of more highly correlated groups, may owe such intermediacy to (*a*) climatic and other environmental causes, or (*b*) to crossing.

(3) The recognition of a species as having a correlated group of characters is often only the expression of the fact that, in a geographical series of groups, each sharing some characters in common with its neighbours but differing in the combination of characters from more remote members of such a series, some of the combinations are more frequent than others.

(4) A group of organisms may exhibit the same characters over all its range or it may be composed of different biotypes, some of which possess characters not found in other biotypes (Shull, 1909, p. 52), or it may be composed of different local races each having a combination of characters different from the others, the total range of variation, however, of all the local races being different from that found in another species (Duncker, 1895).

(5) The relation between two allied species in respect of the differentiating characters may not be the same over the whole of their respective ranges. Thus, Duncker (*l.c.*) finds that the Baltic Plaice and Flounder are more alike than the North Sea forms of these species.

(6) In certain populations in which systematic distinctions

have been made it has been found on analysis that there is in reality a mass of confused character-combination which defies organisation into species or other groups (Lutz, 1909; Crampton, 1925).

The outcome of all this is that the process of divergence seems, on the one hand, to lead to the creation of groups of individuals more or less homogeneous for several characters, which groups may be large and occupy a relatively wide area, or small in size and restricted to a small area; while, on the other, the individuals bearing divergent characters may be less coherently associated, in which case correlation of the characters is less marked or even absent.

When the groups represented by species or the races or colonies of the latter are tolerably homogeneous, we may assume either that extinction or isolation has intervened to secure a certain degree of discontinuity, or that some other basis of correlation is involved. The intermediates we find between such groups may then be the result of some measure of intercrossing, isolation being imperfectly established, or they may be produced by environmental causes, or finally, they may represent the residuum of the stock from which the more highly correlated groups are being developed. Intermediates may be of two kinds—" mid-intermediates ", which are a blend of the characters of two divergent stocks and represent a condition half-way between the two; or else they may be represented by combinations of the actual characters of such stocks. The former may be due to environmental modification or to genetic causes (Imperfect Dominance, etc.); the latter are almost certainly due to genetic causes. Concerning the effects of hybridism in producing intermediacy little need be said here. The incidence of crossing in nature is discussed elsewhere, and it is enough to say that ample experimental evidence shows that, if two species or varieties can be successfully crossed, the offspring often exhibit intermediacy of both kinds in their various characters.

When the areas of distribution or the habitats of allied species are conterminous or overlapping, it is of importance to inquire what the actual relation between such forms may be. Do they invariably show a high percentage of intermediacy in the area common between two species, or do they maintain their specific characters more or less intact ?

When allied species occupy the same terrain, intermediates are often found, as in many land-snails (e.g. *Helicella*). In some cases there is, however, " amixie régionale ". Between two species which occupy the same territory there may be intermediates in one area and not in another. This is well seen in the snails, *Cepea hortensis* and *C. nemoralis*, which show such difference in the French localities studied by Coutagne (*l.c.*), and in the "water-boatmen" (*Notonecta*) observed by Delcourt (1909). I believe that this phenomenon may also occur in the races of a single species. In a study of the banding and transverse markings of the land-snail, *Cochlicella barbara*, of W. Europe (MS.), I have found that in some localities the various types are found in complete distinctness, while in others there is a high percentage of intermediacy. On the other hand, there may be no intermediacy at all reported.

When species show some amount of overlap the same condition is observed. These may be intermediates (*Troglodytes*, Chapman and Griscom (1924); *Junco* (Dwight, 1918)). Rarity of mid-intermediates is seen in the " Flickers " (*Colaptes*), Grackles (*Quiscalus*) and Tits (*Helminthophila*) discussed by Bateson (*l.c.*). Lastly, there may be no intermediacy at all. Bateson (*l.c.*, p. 165) is of the opinion that this is more common than the occurrence of intermediates. I think that, if one confined one's attention to Vertebrata (and possibly Insects as well), this supposition would be correct. I do not, however, believe that it is true of certain invertebrata. Intermediacy in overlapping forms is quite common in Molluscs ; and some very remarkable cases are to be found in the Acmaeas (Limpets) of N.W. America and Australia, the freshwater snails, *Melanopsis*, of Asia Minor, and many other genera. A certain amount of such intermediacy is no doubt purely phenotypic. The fate of hybrid intermediates in nature is very uncertain.

They might maintain their intermediacy for a time, and their numbers might be continually replenished by fresh matings between the parent species. But such matings would have to be a condition of the maintenance of a permanent intermediate population of this origin, for sooner or later one would assume that the parental types would be recovered if no fresh matings between the parent species took place.

II. The Effects of Plasticity

By Plasticity I mean the capacity for receiving structural impressions from the mechanical, chemical and physical factors of the environment, which express themselves in the alteration of the mode of growth, density, proportions, colour and other structural details. Such modifications may be produced either by reactions to specific factors, or they may be passively received by the organism. We naturally exclude lesions of the hard and soft tissues, though it must be admitted that the line between a lesion and other types of modification is not an easy one to draw. The important question in any discussion of these modifications is naturally whether they become hereditary. This question will be considered in Chapter VII. We are here concerned with the incidence of the actual modifications, not with their fate.

There is no need at the present time to illustrate or emphasise a fact that is so widely known as the susceptibility of plants and animals to modification by the environment. What we may attempt is to indicate the limits of plasticity as it may be seen in the various groups of animals and plants. A comprehensive review of the chief groups of plants and animals with some indication of the special features of plasticity in each is a very desirable thing, and a work which should be undertaken at some time. In the compass of the present chapter I cannot provide more than a sketch of such a survey based on the examination of some of the more important groups of animals and plants.

I shall deal very largely with the divergences between taxonomic species and the stability and instability of the characters by which such groups are recognised. Needless to say, we shall simply be taking the readiness or the difficulty with which species can be recognised by the systematist as an index of the plasticity of the characters in which they differ, and much allowance must be made for the undoubted fact that the systematist often fails to distinguish between stable hereditary differences and those that are non-heritable. It is largely admitted that systematic literature is full of species that are simply impermanent "phases" of other more stable groups. In practice, however, the skilled systematist tends to discriminate between these and the more permanent assemblages, but he does so on grounds that are by no means secure and are rarely fortified by experimental evidence.

As we have deferred to a later chapter our inquiry as to whether modifications induced by environmental stimulus are inherited, it may seem difficult to ascertain the general limits of plasticity. If we take the view that all hereditary differences between species, for example, are produced by environmental causes, we will use the antithesis between plasticity and genotypic stability less freely than if we believe that all hereditary change is germinal in origin. On the former assumption a " plastic " species will not be one giving rise to a number of hereditarily unstable environmental forms, but possibly a group of hereditary forms some of which may be worthy of specific rank. Nevertheless, those who believe that induced variation may become hereditary will grant that some forms are more responsive than others to modification by the environment, and that such modification is not always heritable. It is quite evident I think that, whatever the causes of variation may be, some organisms are less responsive than others, and tend to retain their specific identity with greater tenacity. I do not think we can at present speak with certainty as to the origin of variation. Certainly we cannot decide authoritatively as to the origin of any and every heritable variate that is recorded or observed. We can, however, distinguish between greater or less degrees of variability, and if these can be satisfactorily attached as effects to environmental causes, we are entitled to try and ascertain which forms or organ-systems are most responsive.

We shall see in Chapter III. that in the Bacteria the structural features are less constant than physiological characters. We should, however, compare this plasticity with that of more complex organisms with a reservation that the rate of multiplication among the Bacteria is much more rapid, and the number of generations passed through in a given period infinitely more numerous than in other organisms. It will be likewise seen in Chapter III. that the Bacteria are characterised by a very considerable measure of physiological and biochemical differentiation. The most recent tendency is to disregard or to minimise the value of structural characters (Conn and Conn, 1923 ; Reed, 1923, p. 234). The size and shape of these organisms, the flagella of motile forms, and the shape of spores do in certain cases seem to distinguish strains to which the term species may be given. Such structurally differentiated races are, however, less constant than those distinguished by the " physiological " characters. For example, Noguchi (1912), in discussing the various characters of the *Spirochaeta pallida*-group, states that the morphological characters cannot by themselves form a basis of discriminating the various forms. There is thus a suggestion of structural divergence in the Bacteria, but it is but a dim adumbration of that attained in more complex organisms.

The simpler Fungi seem to possess a marked tendency, at least on experimental media, for the form to be rapidly modified. " It is now one of the best known features of culture-work that the form of a fungus can be altered in all sorts of ways by the use of different media " (Ramsbottom, 1926, p. 40). Among the true Fungi, however, taxonomists have employed such characters as the shape, size, colour and surface-character of various parts, *e.g.* of the pileus, stem, gills and volva, for the recognition of species, and these features seem to be fairly constant and not prone to excessive plasticity.

The variability of certain groups of Algae has been studied by Crow (1924, *a* and *b*). It appears that, *e.g.* among the Chlorophyceae, very minute morphological differences may be transmitted for many thousand of generations without change when these organisms are kept as pure cultures. Change in the medium or in other environmental factors will, however, produce a corresponding change in the morphological characters. The same conclusions appear to hold good for the Cyanophyceae. In the latter, however, Crow (1924 *b*, p. 405) is at pains to show that change of the medium does not always bring about a change in the specific potentialities. However much, then, these organisms are susceptible to modification by external factors (and Crow is of the opinion " that all characters might be produced by suitable alterations of the environment " (*l.c.* p. 422)), there is a marked residuum of stability manifest in the Isokontae and Akontae, for instance, in the form of chromatophore, cell, colony and thallus.

It is a significant fact that in the Lichens, which are symbiotic unions of Algae and Fungi, " the Alga is as a rule less affected than the Fungus by the symbiotic union " (Lorrain Smith, 1921, p. 5), and determination of the genera and species of algal elements can sometimes be made. This cannot be done in the case of the fungal element. Whether this indicates a greater plasticity on the part of the latter is not as yet clear. The fungal element is derived from the true Fungi (Eumycetes), and it is not at all certain that these are less stable morphologically than the Algae. The Lichen-plant itself is tolerably stable, and the thallus and certain features of the reproductive system (apothecia and spores) seem to be constant in their specific differentiation. The colour and habit are, however, very variable. In the Bryophyta the leaf and stem of the Moss-plant exhibit plastic responses to, *e.g.*, desiccation. But there is otherwise tolerable stability especially in the sexual organs, and the same is true of the Pteridophyta, in which the variation, mode of growth and the arrangement of sporangia are used by the systematist for distinguishing species. The sexual generation (prothallium) is, however, not subject to specific differentiation.

In spite of that responsiveness to the environment which has given rise to what Vesque has called *epharmonic convergence*, it is nevertheless true that such responsiveness is limited in the flowering plants. " In very few families of flowering plants have the different species assumed approximately the same growth form, or, in other words, acquired in harmony with the same environment the same external form and similar adaptations and habits of life " (Warming, 1909). Striking cases of such convergence are known, but they are by no means common. The tendency to show convergence under uniform conditions is shown in the vegetative form, and in such features as the time of flowering and duration of life. The floral structures are more conservative, and as a consequence they are employed more regularly by the systematist. But although the characters of the shoot and foliage leaves are more plastic, they exhibit a residual individuality which is largely unaffected by external conditions.

Many students have commented on the difficulty of recognising species in certain groups of animals, such as the Sponges, Corals and Actiniaria. Specific distinction among the Hydroidea is manifest in the character of the gonophores, hydrothecae and colony. The polyps, mode of branching and the surface of the colony seem to be less frequently differentiated. Broch (1916, p. 6) has laid stress on the importance of the gonophores as a basis of specific discrimination. Stephenson (1921) states that there is great difficulty in defining species of Actiniaria, unless they are examined alive so that colour and habit can be effectively studied. Much work remains to be done in this field, and apparently it is anticipated that the nematocysts will yield " good " specific characters.

According to Wood Jones (1910, p. 83 and foll.), the vegetative habit of the Madreporarian colony, the character of the corallites, surface-structure and mode of asexual reproduction are very variable, and do not lend themselves to specific differentiation. The habit of the colony is apparently very plastic, and the same species may exhibit still-, rough- and deep-water forms or "phases". The characters of the zooids seem to be the most constant. In the Alcyonaria the polyps, autozooids, siphonozooids and spicules seem to be the chief seat of specific differentiation.

In the higher Metazoa plasticity is of tolerably frequent occurrence. The most regular and striking occurrence is certainly among sessile or slow-moving forms, such as Polyzoa and certain Mollusca. In these it very rarely compromises specific distinction fundamentally; though in the organs principally affected it may do so, as in the case of the shells of sedentary Molluscs (e.g. *Vermetus*, *Ostraea*, *Chama*.) Within a single group, however, its incidence is very anomalous and difficult to associate with any particular habit or structure. In the Mollusca, for example, there is a general responsiveness of the shell to the mineral constituents of the medium or the food. The shell of *Littorina rudis* becomes depauperate or dwarfed in brackish water (Pelseneer, 1920) in divers localities. That of *Cepea* likewise becomes thin when the animal lives on soils poor in lime. Nevertheless Taylor (1894) reports that normal shells are likewise found on such soil. In Cornwall I have found thin-shelled and normal forms living side by side on granite soils. Striking examples of sensitiveness to environmental change are, however, to be found in more active animals We may recall the well-known effects of salinity on *Artemia salina*, of temperature on Lepidoptera (Standfuss; Fischer) and differences of nutrition on *Hyalodaphnia* (Woltereck). Numerous examples of such responsiveness are given by Przibram (1910) and Cuénot (1921). To these we ought to add the less familiar correlation of " climatic gradients " with colour change in Birds (Swarth, 1920, etc.) and Mammals (Sumner, 1923).

It seems, then, that all grades of organisms exhibit plastic responses in some degree. In lowly organisms such as the Bacteria, Algae and Myxomycetes, the structural facies is apparently less stable and readily responds *en bloc* to external stimuli, though in the Algae and Fungi a nucleus of specific constancy is found.

I think we should set aside the idea that plants as opposed to animals are more plastic and responsive. The real distinction seems rather to be between motile and sedentary organisms, as far as more highly organised animals are concerned. In the meantime we should note that, however responsive to external conditions the structure of plants may be, there is even in the lowlier forms a residual stability in certain structures which exhibits specific differentiation. In animals it is a little difficult to make a narrow distinction between those which are specially plastic and those which are not. At the offset one is tempted to state dogmatically that sessile forms (*e.g.* Porifera, Coelentera, tubicolous Annelids and Molluscs, and adherent members of the latter phylum (such as *Chama*, *Ostraea*, etc.) display greater plasticity than actively motile animals such as Arthropods and Vertebrates. Sedentary animals capable of motion, such as many Gastropod and Lamellibranch molluscs and Echinoderms, would occupy a position midway between the groups previously named. I think this statement is true on the whole, in that there is in sessile forms a general plasticity of the skeletal parts approximating to that seen in the growth-form of plants and rarely found among actively motile animals. But on the other hand, many of the latter may display a marked responsiveness of certain parts to special factors (*e.g.* temperature, humidity). This is notably seen among Lepidoptera and Mammals especially with regard to colour; and it is quite likely that a good deal of the variation in dentition (cf. Hinton, 1926, *passim*) and the length of limbs of the latter may be due to this cause.

III. Special Polymorphism

We have lastly to consider a special series of phenomena that tend to make the distinction of species peculiarly difficult, and in certain cases renders the morphological criterion quite valueless. A species is said to be polymorphic when it exhibits a number of diverse characters which are not present either singly or in combination in all parts of the total population of individuals representing the species. Such polymorphism may be very obscure and of a statistical kind. But it may become very pronounced, as when a single character appears in the population in two or more strongly marked mutational phases. The " *Atya* " and " *Ortmannia* " mutants of various prawns of the family Atyidae (cf. Calman, 1910, for a review and summary) are an example of this. Or what we may call " physiological dimorphism " may produce an analogous effect, as seen in *Amblystomum* and its *Axolotl*-stage. More removed still from normal polymorphism and due to different causes is sexual dimorphism, of which numerous instances are available (Coleoptera, Lepidoptera, etc.). I wish to draw attention to the relation of specific differentiation to the latter, and a peculiar difficulty that arises in this connection. Sometimes we find a chain of forms differing in certain characters, the separate links of which chain are individuals of different sexes differing in such a way that, *e.g.*, the female of a species, either permanently or periodically, may exhibit characters commonly found in both sexes of a different species, while the male, likewise permanently or periodically, has a different phase of such characters. A good instance of this is seen in the curious little squids of the genus *Alloteuthis*, the seasonal dimorphism of which has been described by Grimpe (1925). In the summer months the female has a short " tail " (or apical point of the mantle), the male a rather longer one. In the autumn " long-tailed " females appear, though the tail never grows to the inordinate length which it attains at that time of the year in the male. The " summer females " more or less are in the stage of " tail "-development attained by the allied species *A. media*, while the young *subulata* of both sexes, like the latter, have short tails. In the adult male *subulata* the tail is rarely short enough to make it approximate to that of *A. media*. An analogous case is seen in the " water beetles " (Dytiscidae) described by Chateney (1910). In *Dytiscus marginatus* the male has smooth elytra, the female usually channelled elytra, though a few females have them smooth. In *Dytiscus circumflexus* the females have the elytra normally smooth, but a few foreshadow the *marginatus* stage in having them channelled. Apart from these species, which have dimorphic females, there are species in which the elytra are exclusively smooth or exclusively channelled in the female. It must be noted that these peculiarities relate to single characters, and certainly in the case of *Alloteuthis* the two species, *subulata* and *media*, are to be clearly recognised (though not in all examples) by the residuum of *subulata* and *media* characters. We see, however, that interchangeable characters or those borne in common may become restricted (partly or periodically) to one sex. More extreme cases of this phenomenon in which several characters are involved are found in Lepidopteran mimicry groups (cf. *Papilio polytes*, Fryer, 1913).

B

In the preceding sections we have seen the causes that render difficult the recognition of species regarded as groups of varying degrees of distinctness. We have now to see on what grounds the systematist employs the species-concept, and in what sense species can be satisfactorily recognised as " tolerably well-defined objects " (Darwin).

The basis of such recognition is usually some measure of discontinuity in such of the structural features as have been examined, together with a similar measure of difference in habitat or area occupied and physiological attributes. Although, as we have granted, discontinuity is a crude concept, and its arbitrary use in systematics is seen both in the assessment of differences between two phases of a single character and the number of such discontinuous characters which qualify a group for specific or varietal status, nevertheless we repeatedly encounter groups which, subject to this criticism, may pass for discontinuous. Although they are plainly of close relationship, they differ in so many points of structure and distribution and so clearly in each that, though they may have many points in common, we instinctively concentrate on the differences. It not infrequently happens that such forms are distinguished by some critical difference of reproduction or habits. An example of such clearly cut groups are the Mountain Hare (*Lepus variabilis*) and the Brown Hare (*Lepus* (*? Eulagus*) *europaeus*) (discussion on pp. 197-202).

Easy as recognition by discontinuity may be in some cases, in others it is, as we have suggested, very difficult. The subject of continuously and discontinuously related species will be dealt with anon (Chapter VII.). In the meantime we should consider another means by which we recognise definite groups even when continuously related *inter se*.

The two common English molluscs, *Cepea hortensis*, the Garden Snail, and *C. nemoralis*, the Wood Snail, are distinguished as two species, though the total population made up of the two forms includes individuals which are recognised as intermediates. The latter may be "mid-intermediates", that is to say, they represent a stage midway between the two extremes represented by the "*hortensis*" and "*nemoralis*" characters, when most unlike each other. This midway stage may be exhibited in one or more characters. There may be forms in which the general form is not globular, as in *hortensis*, nor expanded horizontally, as in *nemoralis*, and in which the lip is not dark as in *nemoralis*, nor white as in *hortensis*, but pale brown or just suffused with pigment, the mid-intermediacy occurring in the same individuals. Or else intermediates may occur in which, while some of the characters are *nemoralis*-like, others are *hortensis*-like; for, with one exception only, the characters are not restricted to one or the other species but are interchangeable. On what, then, does the practice of regarding the two species as distinct entities depend?

There are two forms of dart (the calcareous pointed rod secreted in a special part of the genital system and discharged against the partner as a stimulus during courtship) which, save in very rare cases, are perfectly distinct in their shape and accessory blades. Pure "*hortensis*" forms have one kind, pure *nemoralis* another. Intermediates of both the types described above have one or the other dart-form, and the more the intermediates incline to one extreme the more sure they are to have the dart of that form. The rest of the internal structure which has been intensively studied by Miss D. Aubertin (MS.) exhibits intermediacy of some kind between the two specific forms. Now in this case we have a critical character, the dart, which shows a clear-cut distinction. In other cases no such critical character or characters are available. Between the common limpet, *Patella vulgata*, and the "flither", *P. athletica*, which I investigated personally, all the characters of the shell and of the internal organisation exhibit intermediacy. But, whenever distinction is made between two forms which are linked by intermediates, it depends upon the fact that in the total population concerned there is a correlation of the differentiated characters of such an order that certain combinations occur more frequently than others, and to these the systematist applies his specific names. In short although, as we have said (p. 11), there is no standard number of characters, differentiation of which characterises a species, and though, in the case of the land-snails above described, discontinuity in the form of the dart does not in some mysteriously essential way constitute a "specific" difference, there is a progressive differentiation and correlation of the differentials, so that, although in closely related forms there may be interchange of characters or many characters shared in common, even these interchangeables tend to separate out and enter into different combinations. Although in many groups of animals and plants there are species designated on a paucity of characters or individuals the value of which we may mistrust, the most critical taxonomy succeeds in revealing a residual individuality based on several correlated characters which may defy standardisation as "specific", but certainly represent "moments" in the process of evolution. I have said above that the two forms of *Cepea* can be distinguished most clearly by the dart, that while in many characters there is intermediacy, in the dart this is practically unknown. I think it is hardly necessary to point out that it is waste of time to try to decide what we should call a form with a "*nemoralis*" dart and several "*hortensis*" characters. The species-concept can only be used in reference to groups of organisms which exhibit a constant system of correlated characters, and when an individual is a *pastiche* of characters from two different systems of this sort, it is most obviously inapplicable. Some systematists follow the practice of regarding certain characters as essentially diagnostic, and of composing keys for the recognition of species within a genus based on a single character. It must be understood that the relationship of such groups of species is highly doubtful, unless such a character is known to be a component of a group of characters which are correlated. If we are to infer relationship from structure the only safe procedure we can adopt is to assume that the closer the relationship the more numerous the characters will be in which similarity is exhibited, and that the wider the evolutionary divergence the more numerous those characters will be in which dissimilarity is seen. As to the truth of this assumption we may well be sceptical in individual cases. It is possible that sometimes closely allied forms may diverge in many structural characters and remotely allied species may resemble each other in very many, but diverge markedly in one or two. It seems to me that in constructing any scheme of classification on a basis of relationship we can only proceed on the assumption outlined above, and regard forms which are fertile *inter se*, which have contiguous or overlapping distribution and resemble each other in many characters, as more closely allied than those which are sterile *inter se*, are not contiguous in distribution and diverge in many characters. When structure is taken as the sole criterion of relationship, it becomes increasingly imperative to use as many characters as possible for diagnosis ; for it actually is found in practice that, if a few characters are taken, the presumed relationships of species within a genus may change according to the character used for diagnosis (cf. Robson, 1921 *b*).

The correlation of characters is, then, a highly important question in any discussion on the origin and nature of species, for it is obvious that, if there were no tendency for characters to be associated in some sort of frequency, it would not be possible to recognise the sort of discrete units with which we are familiar.[1] (The relation between discontinuity and correlation is discussed in Chapter VII.) At the present time our knowledge of the association of physiological characters is very limited, so that the action of correlation can only be satisfactorily studied upon structural data.

Although the investigations of the Biometrical school have supplied us with copious information, it must be admitted in advance that our knowledge of the extent of correlation between the divers parts of any single species is singularly deficient. I am not acquainted with a single species in which all the organs have been explored with a view to ascertaining the amount of variability in the various organ systems, though Weldon (1893) and others have systematically explored single areas or systems.

The general occurrence of some measure of correlation between the various parts of an organism is, as we have said, proved by the fact that we can usually recognise the more or less distinct groupings which we call species, even when the latter are connected by intermediates. Apart from the question of the association of specific characters, correlation has been frequently noted in a general way between pairs of characters without any exact measurement of the frequency of association. A large amount of data of this sort is to be found in Darwin's *Animals and Plants under Domestication* (chap. xxv.). A second source of evidence is to be found in genetic experiments in which certain characters are linked or segregate together and sometimes whole blocks of characters behave in this fashion (cf. Chapter VII.).

Although correlation is a phenomenon of general oc-

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[1] This point was emphasised by Darwin (1875, chap. xxviii.), who fully realised the importance of correlation in species-formation ("Many variations, however, are from the first connected by the law of correlation. Hence it follows that even closely allied species rarely or never differ from one another by one character alone . . .").

currence, its incidence is apparently capricious and its intensity very variable. A few examples drawn from the results of biometric study may serve to illustrate this. Warren (1897) obtained measurements of some 2300 specimens of the shore-crab, *Portunus depurator*, and the following are random samples of correlation coefficients obtained by this author :

Total breadth and frontal breadth	$r = \cdot 14$
„ „ Rt. dentary margin . . .	$r = \cdot 56$
Frontal breadth and Rt. dentary margin . . .	$r = \cdot 03$
Right antero-lateral and L. dentary margin . .	$r = \cdot 74$
„ „ L. antero-lateral . .	$r = \cdot 86$

Weldon (1893), using 2000 examples of another crab, *Carcinus maenas*, worked out twenty-three different correlation coefficients between pairs of organs for two different races (from Plymouth and Naples) with the same general results for the two races.

Again Alkins (1923, p. 27) finds that in the Brachiopod *Terebratula punctata* the correlation of length × width and length × depth is very high ($r = \cdot 9$), that of width and depth is still high ($r = \cdot 8$), while in *Rhynchonella poveti* that of length × depth is low ($r = \cdot 3$). There is likewise evidence that such correlations may be preserved in ontogeny, which suggests that they are permanent racial features.

Alkins and Cook (1921) made similar studies of the small pond and river mussels, *Sphaerium*, and other molluscs. In three species of *Sphaerium* were obtained high values for length × width, length × thickness and width × thickness. Thus in *Sphaerium lacustre* length × width has $r = \cdot 95$, length × thickness has $r = \cdot 90$, and width × thickness has $r = \cdot 92$· In *Clausilia itala* length × width has $r = \cdot 39$, and in *Ena obscura* the same pair has $r = \cdot 36$. I have worked out the values for four characters of the shell and radula in the common limpet, *Patella vulgata*, and find that r varies from ·24 to ·6.

It is as yet uncertain whether the same pair of characters tends to have the same correlation in related species. It may be noted that in Alkins' three species of *Sphaerium* $r = \cdot 90 - \cdot 96$ in all three pairs of characters. The tabulation of Weldon and Warren's results with the Naples and Plymouth races of *Carcinus maenas* and *Portunus depurator* shows very little difference in respect of the nine pairs of characters, the range of difference being ·03 – ·23.

We have seen that the natural populations to which specific names are applied are often made up of more or less discrete elements (elementary species, local races, colonies, etc.). To what extent the characters in which homogeneous species or the subdivisions of more " polymorphic " species differ from their allies are correlated depends theoretically on various considerations, such as the degree of isolation, simultaneousness of origin of the characters in question (see Chapter VII.). Here we are only concerned with the facts of correlation, and needless to say it is impossible to state how high the correlation coefficient of the characters distinguishing species is as a general rule.

What is required is that a large number of species within a single genus should be studied from this point of view, and the average correlation of the distinguishing characters ascertained. In all probability there would be very great variation ; but we have no means of even guessing whether the average would be rather high (say $r = \cdot 7$) or rather low ($r = \cdot 3$). Using another method on somewhat unsatisfactory material, I have ascertained (MS.) that in the common limpet, *Patella vulgata*, and the low-water limpet or " flither " (*Patella athletica*), the most frequent character-associations occur in about 50 per cent of the two populations. It is very probable that in many cases correlation may be very low or absent.

In this connection we must turn aside to examine some of the evidence derived from paleontological studies, to which I have already referred, evidence which seems to minimise in certain groups the importance and frequency of correlation. The classic work of Waagen, Neumayr and Hoernes on form-succession in the Mollusca has prepared us for a view of evolution in which the boundaries of species are indistinguishable. It is preferable, however, to consider those recent studies of " lineages " in which a more detailed analysis of the fate of individual characters is intensively worked out in groups of closely related forms. Unhappily such series are by no means frequent. The following remarks are based on the studies of Swinnerton (1921), Carruthers (1910), and Lang [W.] (1921).

According to Swinnerton (1921), " with the finding of numerous specimens at different levels the boundaries of the species fade away and the distinct characters are seen to be but a passing glimpse of one point in a stream of definite change ". Species thus seen in the passage of time are to be regarded merely as the effect of the imperfection of the geological record. The only reality to the paleontologist is " the series of changes which may be passed through by a given structural element " (*l.c.* p. 77). A similar point of view is expressed by Deperet (1909, p. 187) as the result of a study of Tertiary mammalia. Trueman (1924, p. 355), in a clear account of the species-concept in paleontology, in which the same general view as that of Swinnerton is expressed, stresses the fact that in the Lower Liassic *Gryphaea incurva* the characters representing different lineages are " largely, if not wholly independent of one another ". Employing the terminology proposed by Lotsy, Trueman suggests that a form like his *Gryphaea incurva* may be a " Linneon " or " impure " species composed of freely inter-breeding individuals with interwoven pedigrees. He points out, however, that " whereas Jordanons generally differ from one another in sharply contrasted characters, such as the presence or absence of some contrasted characters, the various members of such groups as the paleontologist is concerned with, merge into one another by imperceptible gradations " (*l.c.* p. 360).

The evidence for the chaotic mixture of characters in the lineages examined by these authors seems to be irrefutable, as far as the organisms studied are concerned. But, without straining the evidence from genetic research, we cannot regard the concept of a continuous flux provided by the paleontologist as universally applicable. The picture indeed reminds us of those series of intergrading forms which the student of geographical distribution often finds. The limpets of the genus *Acmaea* provide examples on the N.W. American coast, where the *persona, pelta* and *testudinalis* groups are found in a continuous series from the Arctic coasts to California. But until such cases are carefully studied by experimental breeding of the " intermediates " and the effects of the environment and heterozygosis exactly determined, it is obvious that we cannot say whether discrete elements are not concealed in the apparently gradational series.

Again, if in the lineages of Secondary corals or Palaeozoic Echini there are no " moments " of stability, no permanent character-associations, one thing is certain—that a great many " species " in other groups have exhibited very considerable stability, and have been recognisable as permanent combination of characters for very considerable periods of time. We may cite a single group of animals in support of this, though very many examples will offer themselves to specialists in various groups. Messrs. B. B. Woodward and A. S. Kennard have devoted many years to the study of the Tertiary, Pleistocene and Holocene deposits of East Anglia, and to tracing therein the origin of the modern land and freshwater mollusca of this area. They find that many modern species are to be recognised from mid-Pleistocene deposits, e.g. *Cepea nemoralis*, *Limnea pereger* and *truncatula*, *Hygromia hispida*, etc. Furthermore, *Corbicula fluminalis*, *Bithynia tentaculata*, *Paludestrina stagnalis* and others are of undoubted Crag origin (Pliocene).

The following suggestion is made with deference to the opinion of the experienced paleontologist. We may reconcile the discrepancy between the view of species put forward by the students of lineages and the undeniable evidence of persistence of definite specific type derived from other data by suggesting that in certain cases, most of which have fallen to the lot of the student of lineages, organisms highly susceptible to environmental influences, of marked plasticity, may give the impression of very imperfect differentiation into species, while others less susceptible and in a more stable physiological condition may maintain specific individuality. The degree to which interbreeding is facilitated or hindered by the mode of life of an organism must also count for a good deal (see Chapter V.). It is true that lineages in other groups than corals have been studied (for example, *Gryphaea*), but, as we have previously stated, there are plenty of modern instances of acute plasticity among sedentary molluscs. Nothing but exhaustive genetic analysis can supply us with either a denial or an affirmation of specific individuality in such form.

The causes of correlation and the means whereby the aggregates of individuals constituting a species or a race come to be distinguished by several correlated characters will be discussed in Chapter VII. It is enough for us at present to establish the importance of correlation as an attribute of species, to have pointed out its capricious incidence, and to have discussed the special paleontological evidence bearing on this subject.

We have thus surveyed some of the salient facts concerning the variability of plants and animals and the circumstances in which taxonomic recognition of species is easy or difficult. In their appropriate place these conclusions will assist us in forming an opinion on the origin of specific divergence with which question the occurrence of correlation, the responsiveness to environmental stimulus and the composition of natural populations is intimately connected. It remains now to deal with a secondary issue of some importance.

Any one who has studied the classification of a number of different groups of animals will agree that it is impossible to make any useful generalisation concerning the parts or organs that are affected by specific divergence. It seems, however, that in the opinion of most systematists the external parts and the reproductive system, when differentiated, yield the best criteria of such divergence, and we should briefly examine the grounds for this opinion.

The majority of species diagnosed by systematists are founded on differences of the external parts. This is mainly due to the practice (very often imposed by circumstances) of examining and describing the external parts only. If we were merely dealing with the products of the systematic convention, there would be no need to discuss the matter. In point of fact the matter is not so simple as this, and it is worth our while to compare the relative variability of external and internal parts a little more carefully.

We may admit in advance, as we have done already, that the divergences between species have no very direct and immediate bearing on the problem of variation. But, speaking generally, taxonomic practice is largely guided by the facts of nature, so that the features singled out by the systematist have some significance. If the systematist happens to consider a diversity of characters, the chance is that the species he diagnoses do represent the lines of evolutionary divergence pretty closely. In the following argument I shall employ systematic data of this kind. My object is to discover if there is in the external, as opposed to the internal, parts of animals any difference in the readiness with which they yield " specific " differences.

Pelseneer (1920, p. 409) has stated that " la grande variabilité de ces appareils ectodermiques se comprendra par la longue hérédité de l'ectoderme, feuillet extérieur des ancêtres phylogénétiques ". We are, in short, to regard external parts (including those such as the radula of Mollusca, which, though actually internal, are nevertheless ectodermal in origin) as most variable because they are derived from the most primitive of the germ-layers. It must be observed that Pelseneer's statement is applied to variability in general, and not to the differences between species. It is of importance, however, to see if his generalisation can be extended to specific divergence.

As far as the latter is concerned I do not think the principle is applicable. Mesodermal structures such as parts of the skeleton of vertebrates and the reproductive organs of Oligochaetes, are subject to marked specific differentiation. Nor are the ectodermal parts, *e.g.* in the

Mollusca with which Pelseneer was concerned, of equal variability. Some facts in illustration of this may be given.

In two closely allied species of a large African land-snail, *Cochlitoma*, which were intensively worked out (Robson, 1921 *b*), the generative organs were if anything more distinctive than the shell. The latter, the radula and mandible, were next in order, the crop, kidney and nervous system (ectodermal in origin) showed still less differentiation, and the rest of the organs scarcely any at all. In forms in which there is no shell, as in certain slugs for example, the external form, surface sculpture " keels ", etc., are often diagnostic of species, but such characters are rarely as clearly differentiated as the genital organs (Ellis (MS.), *Milax ;* Hoffman (1925), *Vaginulidae*). In the carnivorous slugs of the genus *Apera*, exhaustively studied by Watson (1915), we find the nervous system, external form, vascular system, radula, pedal glands and genitalia clearly differentiated, differences in the latter being most clearly distinguishable. The lack of variability and specific differentiation found in the Cephalopod mandible (an ectodermal structure), referred to on p. 50, may be also cited.

Apart from the question whether the ectodermal structures are essentially more prone to specific diversity than those derived from the other germ layers, it seems at present that, in certain groups, *e.g.* the Mollusca, Oligochaeta, Vertebrata, some of the internal parts exhibit specific divergences very clearly, while in others the internal parts are singularly unmodified.

In many groups in which the exo-skeletal parts are complex and diversified, *e.g.* the Arthropoda generally, the Polychaeta and the Echinodermata, it seems that very little differentiation of the internal parts is at present reported. Probably not enough attention has been paid by systematists to the latter to enable us to say that the internal structures are not differentiated at all ; but the present general impression is probably correct in the main ; for in these groups, when the internal parts are intensively studied along with the external, the lack of differentiation in the former is apparent. Thus, in a comprehensive survey of the structure of Holothuria collected in the Pacific, Ohshima (1915) finds uniformity in the respiratory and genital organs, Polian vesicle and stone-canals, while the external shape and size, the pedicels, table-like deposits, rods and calcareous ring, are subject to much specific diversity.

In certain groups of animals some parts or organs are inherently and, for no particular reason that we can at present fathom, less liable to specific and varietal divergence than others. A very interesting case in point is the mandible or horny beak of Cephalopods. These structures are of considerable functional importance to the animal. They should, if adaptation to different articles of diet is an important factor in determining specific differences, show considerable diversity. Yet in the Cephalopoda they are singularly little affected by specific divergence. Through whole families of this class they show either no difference at all or so slight a differentiation that it is only barely appreciable. The radula, on the other hand, is markedly differentiated; though oddly enough in the Cirrhomorpha, in which the radula is almost entirely absent, the mandibles are persistent and non-degenerate (Robson, 1926).

Those parts of the alimentary tract that are primarily concerned with digestion and absorption seem in the present state of our knowledge to be very little differentiated, though allowance must be made for the physiological state of the animal at the time of death. I am not familiar with intensive work on the differentiation of the muscular system, though in certain instances (*e.g.* in the land-snail, *Cerion*, Bartsch, 1920, p. 9) certain groups of muscles are stated to be specifically diversified. Glandular structures, as far as I am aware, usually vary considerably from individual to individual, according to the season and physiological state.[1]

Until the internal structure of those groups in which the external parts are notoriously subject to specific differentiation is exhaustively studied, we cannot decide if the general

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[1] Kleiner (1912) shows that the number of processes of the glandulae mucosae in *Cepea* may be diagnostic of different species.

impression that external parts are more prone to diversification than the internal ones is correct, and if Pelseneer's special hypothesis has any validity. In the group (the Mollusca) which we examined in some detail we found that all the external parts are not equally prone to specific diversity, and that in this and in other groups, internal structures such as the genitalia exhibit a high degree of differentiation. Nevertheless, at present it seems as though the chief seat of specific and varietal divergence is in the more external structures. It may be held that this may be partly explained as a natural consequence of the greater exposure of the external parts to environmental stress. In the main this may be true ; but I suspect that, when more studies of the relative variability of the various organ systems are available, it may be found that a good deal depends on purely idiosyncratic differences.

A far simpler question is that relating to the specific differentiation of the reproductive organs. In those groups in which the latter attain any complexity, that is to say, in which they consist of more than a simple gonad and an oviduct or vas deferens, we find a marked tendency to specific divergence. The divergence may manifest itself in the accessory structures of the genital tract (such as glands, spermathecae, intromittent and receptor organs, etc.), in clasping organs or in structures used in courtship and display. In the species of Trematoda, Nematoda, Oligochaeta, certain groups of Mollusca (Pulmonata, Opisthobranchia, Cephalopoda), the Arthropoda generally, Birds and many Mammals, they attain a high diagnostic value. It is very likely that in certain groups (*e.g.* the Ophidia and Lacertilia among the Reptilia) in which but little serious attention has been paid to them, they will be found to be of more specific value than is at present realised. Although in a general way we may say that increase in complexity and increased specific diversity of the reproductive apparatus is associated with coitus, there remain some anomalies which await a solution. In several genera of Prosobranch Mollusca (e.g. *Buccinum*), in which fertilisation is internal and the male has a penis, the latter and the vagina of the female exhibit very little, if any, specific diversity. Again, in many Insects (Boulangé, 1924) it is noteworthy that it is the male, and not the female, apparatus which is differentiated. In Chapter V. further consideration is given to this point, and to the importance of differences in the genitalia as a factor in isolation.

CHAPTER III

PHYSIOLOGICAL DIFFERENTIATION

NO one will doubt that the vital substance of plants and animals, their tissues and their functions, are differentiated in the same general way as their structure. In one way or another the fact has impressed itself on the notice of mankind, and our recognition of it emerges in agricultural practice and tradition, in medicine and in other human activities.

In the present chapter I shall attempt to review the incidence of certain types of physiological differentiation[1] with a view to ascertaining if the latter is in any sense correlated with structural differentiation, and if it is exhibited by any particular activity or part of the living substance.

The idea that the intimate constitution and the functions of living organisms are taxonomically differentiated in the same way as their structure is by no means a new one. Fifty years ago Jaeger (1876), as the result of a study of the organs of taste and smell in the Vertebrata, laid it down that " es gibt nicht bloss Individual-, Varietäten-, Rasse- und Speciesgerüche, sondern auch Gattungs-, Familien-, Ordnungs- und Klassengerüche ". Since that date the growth of experimental physiology and medicine has furnished us with a large amount of confirmatory evidence, and the notion of physiological differences between species has at the present time a wide acceptance. The concept of purely physiological differentiation has also been extended to more profound biochemical differences in the cytoplasm of organisms.

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[1] *Physiological* is used in this discussion in a wide sense, and is applied to certain differences which might be defined with greater precision as biochemical or biophysical.

There is a sense in which biochemical differentiation may be considered as proved without further demonstration. We cannot consider structure *in vacuo* without taking into account the complex processes by which it is produced. Every structural change must, with a few exceptions, be founded in some alteration of cellular activity. Whatever the ultimate origin of such change may be, it is obviously translated into structure through the medium of physical and chemical activities. Similarly the latter seem to play an important part in determining the whole or a part of certain differences between species, *e.g.* in distribution, habits and the capacity for fertilisation. These matters are more suitably discussed in other places in this work, while our present concern must be with physiological differentiation in the narrower sense.

If we thus are compelled to regard the sum total of an organism's attributes—metabolic, structural, habitudinal and reproductive—as the expression of its fundamental biochemical and biophysical constitution, it follows that the *differences* which we recognise as specific at the structural level must be likewise founded on more deeply stated differences. As we have already seen (p. 23), it is by no means easy to refer the structural and other differences between species of plants and animals to more remote differences in their constitution. The physiological differences between species with which we are best acquainted are those of metabolism and its products and special activities, such as ability to ferment certain substances, pathogenesis, reaction to temperature, light, etc., and at present I shall confine myself to a consideration of these properties.

A study of the Bacteria gives us convincing proof that the constituents and activities of the cytoplasm of organisms are susceptible to a very considerable amount of differentiation, giving rise to groups analogous to species distinguished by structural characters. Among these organisms are to be found groups or strains differing in a variety of characters which are regarded as species and are designated according to the ordinary binominal system. Various authors have questioned the validity of treating such strains as species; and in particular, Minchin (1912, p. 141) has attempted to find a basis for this scepticism. Speaking of the effect of syngamy as opposed to simpler methods of reproduction, he says: "If Protist organisms placed under slightly different conditions of existence tend to vary in their characters as a direct consequence of environmental influences, syngamy would check any such tendency, and would, on the contrary, tend to keep a given species, constant and uniform in character, within narrow limits. Were there no intermingling of distinct strains, such as syngamy brings about, individuals of a species subject to different conditions of life would tend to give rise to divergent strains and races; syngamy levels up such divergencies. . . . If this supposition be correct, it would follow that no true species could exist until syngamy had been evolved; and if it be true that no syngamy occurs in organisms of the bacterial type of organisation, then such organisms must be regarded as having diverged under direct environmental influences into distinct races and strains, but not as constituting true species. The species of Bacteria would then be comparable to the races of the domestic dog, rather than to the natural species of the genus *Canis*."

From this opinion I venture to dissent for two reasons. In the first place, the susceptibility of Bacteria to modification by the environment cannot be taken at its face value and compared with that of more complex organisms, as the rate of multiplication of the Bacteria is infinitely more rapid. Secondly, although Bacterial strains are often very plastic, they sometimes manifest stability in spite of a change of medium (cf. Massini in Dobell, 1912, p. 329). If, therefore, we find groups or strains differentiated in several characters maintaining their individuality for even a moderate period of time, they may be as fairly termed species as are equivalent groups in other classes.

In the Bacteria, structural characters are exceedingly unstable, and far greater constancy is found in their physiological and biochemical properties. The classification of these organisms and the discrimination of species among them is a matter of very great difficulty, and I believe there are many bacteriologists who are sceptical as to the value of any basis of classification. There is, however, a consensus of opinion as to the value of physiological and biochemical characters, and as a result the latter figure prominently in the scheme of classification put forward by the American Society of Bacteriologists (1920). In this scheme the following characters are used for diagnosing species along with cultural and morphological ones: temperature, chromogenesis, production of Indol and H_2S, relation to Oxygen, diastatic action, action on milk, nitrate-production and fermentation. These are stated to be more constant than the cultural and morphological characters. It should be also noticed that, not only are such characters more constant, but they also differentiate strains which are sometimes structurally indistinguishable. When, however, a question of chemical reaction is involved, the range of such reactions is very varied. Thus Reed (1923) shows that in the *Bacillus coli* group there is a very wide range of fermentative activity, some forms fermenting only certain monosaccharides, others fermenting many disaccharides and monosaccharides. Moreover, the stability of the above characters is by no means absolute. One of the most characteristic features of Bacteria, their pathogenetic activity or *virulence* (which in all probability has a biochemical basis), is liable to "attenuation", and is incapable in many cases of maintaining its specific stability. Certain forms can be cultured for a long time, almost indefinitely, without losing this power, but in others again it may be reduced, or even lost altogether. Thus the pathogenic *Spirochaeta icterogenes* of Man shows very marked weakening in culture and in the kidney of the Rat (Zulzer, 1925, p. 1649). On the other hand, virulence can be increased in a weakly virulent strain by "passage" through several animals, and in the same way a bacterium which does not normally ferment a given substance may be "trained" to do so by being subcultured and progressively accustomed to the substance in artificial media (cf. Dobell, 1912, Art. 2, *passim*).

The agglutination test is another important method of distinguishing species of Bacteria; but its use has revealed the fact that strains of a species otherwise constant (e.g. *B. coli*) may give diverse reactions. It is also claimed that the same species may contain strains of diverse virulence, some acute, others mild, so that we may have, as in higher organisms, " aggregate " and elementary species. Uhlenhuth and Haendel (quoted in Hindle, 1912, p. 196) have shown that in the Spirochaeta local forms of the same general type of disease may be distinguished by different immunity-reactions on the part of the causative organisms (Spirochaetes of European, African and American Relapsing Fever).

That there can be purely pathogenic races or species of Bacteria is apparent from the work of Uhlenhuth and Zulzer (1922), who showed that, while the so-called *Spirochaeta pseudoicterogenes*, a free-living form, and the pathogenic *S. icterogenes* are morphologically identical, they have different serological reactions, while the former can by " passage " acquire the pathogenic properties of the parasitic form.

While admittedly unstable in many cases and susceptible in general to environmental influence, the vital activities of the Bacteria are obviously subject to a differentiation of a physiological and biochemical nature, which is accompanied by a smaller measure of structural differentiation. In view of the lack of a universal criterion of specificity, it is plainly waste of time to discuss whether the strains or races are species or not. It is sufficient to say that they show the same tendency as more complex organisms to become divisible into discrete groups differing in several characters which appear to be correlated. Such groups are, when considered relatively to higher organisms, unstable; but as long as they are constant they appear to present us tolerably well-defined groups as in other organisms.

The chemical activities of the Bacteria afford, according to Reed (1923, p. 234), some examples of the specificity of enzymes, in so far as the latter react with particular chemical compounds and fail to react with others. Unlike the majority of the reactions of the Bacteria the enzyme activities are constant, though they may be increased or suppressed by environmental modification. The value of this analogy is, however, doubtful; for Bayliss (1919, p. 135) produces evidence that the doctrine of the extreme specificity of the enzymes cannot be acknowledged.

The Protozoa retain a certain capacity for what we may infer to be purely physiological differentiation. In the pathogenic Trypanosomes, Minchin (*l.c.*, p. 162) observed that various forms of *T. brucei*, which are morphologically very alike, inhabit various hosts, and cannot be transferred from one to the other except after prolonged culture on artificial media. As in the Bacteria, virulence and other properties are unstable in these forms and can be experimentally modified. Wendelstadt and Fellmer (1910) showed that the common non-pathogenic *T. Lewisi* could give rise to a pathogenic race by " passage " through the Grass snake; while Gonder (in Hindle, 1912) conclusively proved that the power of resisting arsenophenylglycin acquired by *T. Lewisi* and retained after " passage " through a large number of rats was lost, while the Trypanosome passed through a developmental cycle in *Hematopinus spinulosus*.

In considering the Bacteria and Protozoa, we saw that their activities which are subject to differentiation are of two kinds. We have, on the one hand, susceptibility or reaction to specific tests, or specialised activities such as fermentation. On the other are more generalised reactions of the whole organism, such as occupation of specific hosts with or without pathogenesis. No doubt the latter kind is merely the result of a complex series of individual reactions. To the latter, however, the somewhat loose term physiological species is given, and it must be noted that the same term is sometimes applied to similar total reactions of the whole organism among the Metazoa. Occupation of different hosts or habitats without corresponding structural diversity is sometimes regarded in this light, and Appellöf (1912) has referred to " physiological species " in describing the differentiation of races of marine organisms. In the Bacteria and certain Protozoa we have seen that races or species identical in structure may exhibit obvious biochemical differentiation. Here the differentiation is founded on verifiable physiological or chemical reactions or on differences, *e.g.*, in virulence. The same phenomenon has been recorded among Fungi by Dox (in Ramsbottom, 1926, p. 43). But I do not think we ought to assume that difference of habitat in the Metazoa is necessarily an indication of physiological divergence. A species of Copepod, for example, may have representatives in cold and warm water; but it does not follow, unless we have experimental evidence to prove it, that the cold water individuals cannot easily accommodate themselves to warm water. Their occurrence in cold water may simply be a distributional accident.

In any case I think we must recognise the fact that the "physiological races" of lowly organisms—Bacteria, Protozoa and Fungi, for example—are highly susceptible to modification by the environment. In addition, as Ramsbottom (*l.c.*, p. 42) has clearly shown, we have to face the probability that many morphological species, *e.g.* of Fungi, can be resolved into a large number of pure lines, the distinction of which depends on their occupation of different hosts. Gaumann, for example (in Ramsbottom, *l.c.*, p. 43), found that *Peronospora parasitica* could be resolved into more than fifty such strains which occur on different members of the Cruciferae. Levaditi and Twort (in Dobell, 1912, p. 217) postulate this same phenomenon in Trypanosomes. In other words, the morphological concept of the pure line finds its parallel in the "physiological race"; and if, as seems likely, the "Linneon" can be resolved into a large, possibly indefinite, number of such strains, the concept of species in any save the most arbitrary and conventional sense must in such cases cease to have any significance, just as at the morphological level we sometimes, in dealing with "polymorphic" species containing a great diversity of genetic elements, have to fall back on the single character as a systematic unit.

In describing in some detail the specific and racial differentiation of the various physiological activities of the Bacteria and other lowly organisms, I do not of course wish it to be understood that this type of differentiation is a unique property of such organisms. The obvious reason for stressing the case of the Bacteria is to show that the capacity for the specific or racial differentiation of special activities which, in varying degrees of distinctness, is found in the tissues and organs of the higher plants and animals, and which we shall study in detail shortly, is resident in the structurally undifferentiated organisation of the Bacteria.

In Chapter I. it has been suggested that there is a tendency for some of the metabolic activities and products to exhibit a differentiation that accompanies the morphological specific differences in higher plants and animals. We must now examine the available evidence for this suggestion in detail; and before doing so it will be necessary to make some preliminary observations.

In the first place, as at the morphological level, so in respect of its physiological properties the organism exhibits individual fluctuations. Marked differences of this order are known in the hæmolytic and precipitin reactions of the blood of various animals, while individual idiosyncrasy in immunity from or predisposition to certain diseases is familiar to all. Such phenomena as these led Fick (1907) to speak of the " spezifischer Protoplasmart des Individuums ". Similarly Uhlenhuth and others have shown that in different tissues of the same individual a given substance may vary in respect of its chemical composition. Uhlenhuth (1900) showed that the albumen of hen's blood differs from that of the egg. Wells (1925 *a*, p. 73) has pointed out that cows' milk contains four different proteins which are distinguished immunologically and chemically. Blackman (1921, p. 2), in criticising the classical work of Reichert on the specificity of plant starches, makes the obvious objection that no details were given in that work as to the part of the plant from which the starch was obtained (" except that it came from an area subserving vegetative reproduction "). The varying distribution of a metabolic product is well shown by the work of Wigglesworth (1924). In the butterflies, *Pieris brassicae* and *Vanessa urticae,* while the total quantity of Urea is the same, it is found in the wings of the former, but not in those of the latter. The figures supplied by this author are very instructive, and as a large number of individuals were apparently used (though the exact number is not given) and various developmental stages were studied, they are free from any doubt on the ground that individual or periodic fluctuations may be responsible for these differences. In *Pieris brassicae* the male pupa just before emergence shows the following values for Uric Acid (in mgm.):

Gut.	Wings and thorax.	Abdomen.
1·02	·51	·56

In *Vanessa urticae,* on the other hand, the values are ·32 for the gut, ·00 for wings, and 1·52 for thorax and abdomen respectively, at the same stage of development. An adjustment of these figures for size might have placed the difference entirely above doubt; but the differences of distribution in the various organs are so marked as to render such a correction almost superfluous.

The study of physiological and biochemical differences between allied species labours under a rather serious disadvantage. The investigations from which we can obtain such data are not, as a rule, planned with this special object in view. They are usually studies in comparative physiology rather than essays in physiological taxonomy. As a result there is a lack of information as to the range of variability in any given substance or reaction in morphologically allied species. Similarly too little attention is paid to such sources of difference as diurnal, seasonal and metamorphic change, sexual differences and the effects of captivity on experimental animals. Simpson and Galbraith (in Winterstein, 1910, p. 55), for example, have shown that the temperature of the Starling has a daily variation of about 3·5°C., the daily rhythm differing in various kinds of birds. In the case of metamorphic changes I have shown (1911) that the constitution of the blood of moulting Crustacea differs from that observed between the moults. Such examples are of course familiar, but they serve to show that great care has to be taken in interpreting the recorded physiological differentia of allied species.

Again, there are instances in which a whole group of species within a genus will give the same reaction to a chemical test (cf. Lorrain Smith, 1921, *passim*). It must not, however, be inferred that, because they give the same reaction to one test, they will do so to all.

I ought perhaps to point out that the term " specificity " is sometimes used in a different sense from the one with which we are here concerned. If the tissues or the metabolic products of various animals are subjected to certain tests, and the reaction to the latter is different in the various cases, it is said to be " specific ", even if the animals used are members of different families or orders. This generalised use of the term is, of course, quite in order ; but we have to distinguish between such a use and the sense in which it is applied to differences of reaction between species of the same genus. By far the larger amount of data available for this study are observations on rather distantly related organisms, and there is serious need of studies on species which from their structural characters appear to be closely allied. The lack of knowledge of this sort is a serious limitation, and any investigator who takes up an extensive study of this sort on closely allied species will be doing a valuable service.

There can be little doubt that differentiation in respect to physiological and biochemical properties is a well-marked feature in groups of higher taxonomic status than species ; and it is worth while to consider some examples of this.[1]

Landsteiner and Heidelberger have examined the hæmoglobin of various mammals in respect of (A) their mutual solubility (1923 *a*), and (B) their immunisation reactions (1923 *b*). With regard to the former, it is stated that : " The rule of addition of solubilities is applicable to the differentiation of the oxy-hæmoglobins of not too closely

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[1] E. W. Junk's valuable *Tabulae Biologicae* (1926) was received too late for consideration in this and subsequent parts of this chapter.

related species ", addition of solubilities being obtained between horse and dog, but not between horse and donkey. As the result of the second series of observation (on representatives of various genera), differential results were obtained, and it is apparent that " the serological findings are a proof that the crystallographical findings of Reichert and Brown are due to chemical differences in the hæmoglobin ".

Of equal interest is the work recently carried out on the spectroscopic analysis of various hæmoglobins. As long ago as 1876, Sorby showed that the hæmoglobin spectra of various forms of life were not the same ; and in recent years this field of study has been reinvestigated by Vlès (1922) and Barcroft and his fellow-workers (1924). The latter found differences in the position of maximum intensity of the *a*-bands of oxy- and carboxyhæmoglobin in a number of different animals. These authors state that the differences are (*a*) devoid of phylogenetic significance, and (*b*) subject to marked individual variation, " the differences between individuals looming larger than those between different species ".

Differences of the same order are recorded in the chemical constitution and antigenic property of albumen of the duck's and hen's egg by Dakin and Dale (1919). Ritchie (1925) has investigated the amount of lactic acid in the muscles of various vertebrata during *rigor mortis*. He finds that the difference between the Hake and the Haddock in this respect are greater than that between the Hake and Cod, and makes the suggestive observation that the muscles of the more active animals contain more of this acid than do those of the less active.

Hunter and Ward (1919) have made estimates of the urinary constituents in certain mammalia. The " uricolytic index " is given as " the ratio . . . of allantoin nitrogen to the sum of uric acid and allantoin nitrogen only ". The results are devoid of phylogenetic significance, the Rat (*e.g.*) having the same index as the Dingo, and the Mouse the same as that of the Dog. These authors state that the individuals of a given species vary very little, and always conform to a single type. Nevertheless, they quote other authors who maintain that the index may vary very considerably.

In particular, they refer to Benedict's statement that in the Dalmatian Dog the purine metabolism approaches the human index nearer than that of any mammal below the Chimpanzee. They suggest that special circumstances (*e.g.* domestication) may lead to modification of the index.

In presenting some data from which we can decide how far the morphological differences recorded as specific by the systematist are accompanied by analogous physiological differentiation, I have adopted the following arrangement of the matter: (1) Proteid specificity (including the immunity-reaction[1] and hæmoglobin characters), (2) specificity of certain non-proteid substances, (3) of the metabolic processes, (4) of specialised products (snake and arachnid venoms), (5) of miscellaneous reactions, etc., and (6) of processes involving one or more of the above-mentioned types of differentiation, but of a complex nature and possibly dependent on other factors. The latter include: (*a*) graft-reactions, and (*b*) reproductive capacity.

(1) The study of immunity-reactions has been a very fruitful source of knowledge as to the differentiation of the living substance of species of higher animals and plants. But it is not at all clear how far the differentiation which it has revealed is characteristic of the species within one genus, and how far the "species-specificity" of the immunologist is the same as that of the zoologist and botanist.

Tested by their immunity-reactions, the proteins of animals and plants show a very considerable amount of differentiation as compared with the water, salts and carbohydrates. According to Wells (1925 *a*, p. 63) the latter show no differentiation, while that of the lipins is limited. The nucleic acid is similarly very little diversified in this respect, though animal and plant nucleins differ. As a result, Loeb (1916) and Wells (*l.c.*, p. 65) lay it down that biological specificity depends on the chemical individuality of the

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[1] I am unable to state whether all the substances, the activities of which are involved in the precipitin- and anaphylaxis-reaction, are proteids. Loeb (1916, p. 61) evidently believes that they are of this nature. Alternatively they may be attached to the proteids.

proteins, it being known that an enormous number of different protein compounds can be formed from a limited number of amino-acids. According to Pick (in Wells, *l.c.*, p. 76), it is not only the number and proportion of the radicals in the protein molecule which determine specificity, but their arrangement.

When Loeb (1916, p. 68) and Wells (*l.c.*) speak of the difference in proteins "determining" the heredity of a genus or the biological specificity of organisms, I think they are making an unwarrantable assumption. It is safe to say, as Loeb (*l.c.*) suggests in a later passage, that difference in proteins " may give rise to the specific . . . immunity reactions ". But I do not think that we are justified as yet in arguing from the differences in protein-constitution to the "biological reactions" or " biological specificity ", by which I infer these authors mean the total expression of specific difference. I speak with diffidence on this subject, but it is possible that we might, with some show of reason, argue that the differentiation of the proteins is influenced by differences in habit, food, etc. At any rate the causal relation suggested by Loeb and Wells is far from being proved.

Now although immunity studies show in an impressive fashion that parts of the vital substance are subject to marked differentiation, the issue is by no means clear as far as species of the same genus are concerned. In the first place, it seems that the same protein may be distributed through many different species (Wells, *l.c.*, p. 68). The latter author and Osborn have shown that chemically and immunologically the legumins of peas, vetches and horsebean are similar; but that two proteins from the same seed may have different chemical and immunological properties. These considerations must put us on our guard against assuming, on the one hand, that the proteins are always differentiated, and that those of a single individual must always have the same immunological activity.

The extent to which closely allied species are differentiated in this respect is very obscure. " Species specificity " is more often than not used in the general sense criticised above as implying difference between genera or families.

The array of data on the precipitin reaction marshalled by Nuttal (1904) is our chief source for facts concerning allied species, *i.e.* species referred to the same genus.

We may accept the statement of Nuttal (*l.c.*, p. 409) that "the degree and rate of blood reaction appear to offer an index of relationship; in other words, closely related bloods react more powerfully (yield more precipitum) and more rapidly than do distantly related bloods, provided the latter react at all". The data set forth in detail in the tables in Nuttal's book show on the whole a certain steady difference between species of the same genus. We should, however, qualify this statement by saying that some species do not always show definite differences. For example, in *Cercopithecus* (tested with "monkey" blood), of which twelve species in all were examined, three groups of 4, 2 and 2 species respectively had each the same reaction, while in certain cases the individual differences are fairly considerable (e.g. *Troglodytes*, p. 222). The general impression obtained by analysis of the species of this same genus is of a fair amount of irregularity in distinction, and in certain cases one would wish to see the results amplified by the examination of more individuals. These criticisms do not, however, invalidate the general proposition that the results of the precipitin reaction are in agreement with systematic, *i.e.* structural, distinction.

The results obtained by Nuttal have been confirmed recently by Boyden (1926) as far as the correlation between difference in blood reaction and the broad lines of zoological classification is concerned. They are criticised by Wells (*l.c.*, p. 54) on the ground that the estimation of the bulk of precipitum is a crude method. The case cited by Wells seems, however, to exaggerate rather than diminish the differences between the forms investigated.

The work of Reichert and Brown (1909) on the specificity of hæmoglobin being less generally known requires a little more detailed account. These authors have shown that the hæmoglobins of a large number of vertebrates, as determined by crystallographic methods, are specifically distinct, the differences extending to species of the same genus. It is perhaps relevant at this stage to point out it is the proteid of the hæmoglobin (globin) which exhibits the phenomenon of specificity, and not the hæmatin, which is, as far as we know, identical in all animals (Barcroft and others, *l.c.*, p. 81). The crystallographical character which, according to Reichert and Brown, shows the most constant specific differentiation, is the axial ratio. Crystals of the blood of different species may also differ in habit; but the species of a given genus usually agree in the system (*i.e.* whether the latter is orthorhombic, monoclinic, etc.). Sometimes species belonging to the same genus differ in respect of the angles (e.g. *Papio babuin* and *anubis*).

The results obtained justify in a measure the author's contention that there is a close parallelism between the hæmoglobin specificity and the morphological differentiation of the forms studied. But in the first place, only some sixteen genera are dealt with in which more than one species is available for comparison. In the second place, we find no data as to the range of variation (if indeed this is to be expected) within single species. Thirdly, anomalous cases occur. With regard to the axial ratio the Dingo is more unlike its morphological associates, the true Dogs, than is the Silver Fox (*Urocyon*); while the Ocelot (*Felis pardus*) is more unlike the other species of *Felis* than is the Lynx. The Guinea Fowls have an axial ratio more like that of the Ostrich than that of *Gallus* or *Collinus*.

(2) A demonstration of "species specificity" in the taxonomic sense of other substances than proteids is due to Reichert (1919). This author undertook an investigation of the starches of plants in addition to the hæmoglobin studies already described. The starches of species referable to a large number of genera were studied with regard to (1) the degree of polarisation; (2) temperature of gelatinisation; and (3) reaction to certain reagents (including iodine, chloral-hydrate, chromic acid, etc.). Without going into extensive details, it may be said that the properties in question exhibit the same general specificity as the hæmoglobin crystals,

though the criticisms of Blackman (*l.c.*) appear to me to be of importance. In certain cases, however, the properties and reactions of the starches are identical in species of different genera, and the species of a given genus do not always differ *inter se*; *e.g.* in the reaction to Ferric Chloride[1] the four species of *Castanea* which were studied are alike, as are some species of *Lathyrus* and *Phaseolus*. In other words, there is no constant parallelism between the starch properties and morphological differentiation. In a second instalment of the same work, Reichert deals with the same properties in the starches of hybrids. Concerning these observations, we may briefly state that the hybrids are indifferently like one parent or the other, intermediate or react less or more markedly than do the parents.

Riddle and Honeywell (1923), working on the blood-sugar of pigeons, found that during mid-ovulation the common pigeon has an average of 208 mgm. per 100 c.c. of blood, while the ringdove has 176 mgm. (*l.c.*, p. 345). These figures are weighted by some uncertain cases, and I should rather put the average at different figures. Differences were also observed between hybrids and "scragglies" (certain mutants of the common Pigeon). The figures in this case are not very numerous.

(3) Quantitative estimates of the processes and products of metabolism in allied species have been made from time to time. The following examples are a fair index of the typical results attained :

CO_2 output (Mgm. per kgm.) at C°

(Vernon in Winterstein, 1910, p. 33).	At 2°	15°	20°	27°
Rana temporaria . .	62	101	139	284
,, *esculenta* . .	25	100	110	152

Mean Body Temperature (*C.*) (*Simpson and Galbraith in Winterstein, l.c., p.* 54)

Fowl . . .	41·44
Bantam . . .	41·48
(Duck . . .	41·52)
(Dove . . .	41·10)
(Hawk . . .	41·43)

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[1] As recorded graphically.

"Critical" Temperature (Bachmetjew in Winterstein, l.c., p. 85)

Vanessa levana	–12·8 *c.*
" *atalanta*	– 1·7 *c.*

Temperature at which Animals lose capacity for Response to Stimulation (*Vernon, l.c., p.* 91)

Rana esculenta	38·5-42·0
" *temporaria*	35·5-39·5
(Bufo	38·0-43·0)
(Axolotl	36·0-39·5)
(Land tortoise	42·5-52·0)
(Water tortoise	43·5-45·5)

Hyman (1919), in studying the differences between old and young specimens of Planarians with regard to the amount of oxygen consumed, found that there are differences in the amount consumed per ·5 kg. weight between *Planaria velata* and *maculata*, while *P. dorato-cephala* has a consumption ranging between those two species. Shelford (1913) found that the land-snail, *Polygyra fraudulenta*, differs from *P. thyroides* and *palliata* in that it is more immobilised by "dried" air than those species.

(4) In the Plant and Animal Kingdoms there are produced probably as by-products of metabolism a number of substances which in certain groups are put to specialised uses. These are the products of glandular tissue, or are carried in a more or less loose state by the body fluids. Among these are some which are recognised as exhibiting a certain measure of specificity, and I propose to examine in detail a single group of these, viz. the snake poisons, to which a considerable amount of study has been devoted by such workers as Phisalix, Arthus, Flexner and Calmette. These substances, which are produced by the supralabial glands, have been analysed from the point of view of their composition, their actual lethal effect and their action on alien tissues. There is apparently a very great variability in the composition of these venoms. They appear to be mainly formed of albumins, mucins, ferments and various salts, the active principles of which may be cytolytic, neurotoxic, agglutinative, etc. The various substances do not

occur conjointly in each species, nor are they found in fixed proportions. Certain main " principles " are characteristic of definite taxonomic groups, but as far as can be judged from lethal effects, the venom of a given species may possess (*e.g.*) more than one lethal principle. Thus while the Colubridae, Hydrophiinae and Elapiinae are characterised by the possession of strong neurotoxic venoms, those of the Vipers are coagulant or hæmorrhagic (Phisalix, 1922, p. 773). The venom of *Crotalus terrificus* (Viperidae) possesses both neurotoxic and coagulative principles, and the same is true of *Naja naja* (Do Amiral, 1925, pp. 10-13).

In judging the specific distinctness of venoms from their lethal effects, it should be recognised that they vary according (*a*) to the method of introduction, and (*b*) to the animal on which they are used.

Do Amiral (*l.c.*, p. 8) gives the following data of the minimum lethal dose (in mgm.) as observed from intravenous injections on pigeons and rabbits :

		Mgm.
Pigeon :	*Bothrops insularis*	·004
	,, *atrox*	·010
	,, *neuwiedii*	·015
	,, *alternata*	·017
	,, *jararaca*	·020
	,, *jararacussu*	·020
Rabbit :	*Crotalus adamanteus*	·200
	,, *terrificus*	·250
	Bungarus candidus	·040
	,, *fasciatus*	·700
	Naja bungarus	·350
	,, *naja*	·250-·500
	Bothrops insularis	·050
	,, *atrox*	·070
	,, *alternata*	·300
	,, *jararacussu*	·300
	,, *jararaca*	·350

The number of subjects used is not given ; but the writer states (p. 7) that the results are in accordance with those of other workers.

Judged by the clinical symptoms there are certain similarities between venoms "principally when the snakes which produce them belong to related species or genera" (Do Amiral, p. 17). But while the venom of *Crotalus adamanteus* causes local pain and hæmorrhage, these symptoms in *C. terrificus* are entirely absent. *Bothrops jararacussu* venom produces disorders absent in other species of that genus; but the various species of that genus and *Bungarus* do not differ in the clinical symptoms.

The serological phenomena have been considered by Phisalix (*l.c.*), Arthus (1911) and others. Phisalix (*l.c.*, p. 772) considers that the toxic action of viper venom is specific. Calmette (in Phisalix, p. 773) does not allow a strict specificity. He claimed that anticobra serum (*e.g.*) can neutralise other venom. The matter was reconsidered after much discussion by Arthus (1911), who concluded that, with certain reservations, the action of anti-venom sera is completely operative only over the special venoms from which they have been prepared. That the action of such sera is not absolutely specific (in the systematic sense) is plain from the following observations of Noguchi (in Phisalix, *l.c.*, p. 780): One c.c. of serum prepared from *Ancistrodon piscivorus* delayed *in vitro* the action of 40 " doses " of *A. piscivorus* venom; but it also had a similar effect on 4·2 " doses " of *Crotalus adamanteus* venom and 4·4 doses of *Naja tripudians* venom.

Among other animal poisons an analogous lack of strict specificity was found by Houssay (1916) in the venom of spiders. Rabbit serum immunised separately against *Araneus amaurophila* and *erythromelo* neutralised not only the venom used to prepare the serum but also the other venom. Neither, however, neutralised the venom of *Latrodectus mactans*.

It is probable that the composition and lethal effects of the venoms of allied species are not as yet exhaustively known. In general there is no very close parallelism between morphological differentiation and the activities of the venoms in question. The complex of physiological activities found in them does not seem to manifest any differentiation analogous to the phylogeny of the Ophidia generally. But the activity of the poisons does seem to differ in a broad way from species to species, though the differences are often so slight as to produce no differences in kind in the clinical symptoms.

(5) In this section we may briefly detail some miscellaneous instances in which differences of reaction or other activities have been recorded between allied species.

Plateau (1872) found that the resistance to magnesium chloride in excess differed in various species of *Cypris*, and that species of certain genera of water insects (*Dytiscus*, *Agabus*, *Hydroporus*, etc.) differed in the time that they could live out of water. The brackish-water snails, *Paludestrina ulvae* and *ventrosa*, differ in the extent to which they can tolerate reduction of salinity (Robson, 1921 *a*).

In addition to exhibiting differential reactions to substances and conditions which may be normally or occasionally met in their habitual environment, species of the same genus sometimes react differently in experimental conditions to substances not normally present in their medium. Such reactions are in a certain sense significant, as they may indicate constitutional differences of a general nature likely to be of importance in determining distribution. Thus Child and Hyman (1920) have shown that *Hydra vulgaris*, *oligactis* and *viridissima*, differ in their general excitation and susceptibility to anæsthesia and muscular paralysis as produced by alcohol, etc.

Mention has been already made of differences in various strains or species of Bacteria with regard to their fermentative properties. Similar diversity between the species of a single genus among higher organisms have been recorded by Castellani and Taylor (1922) among Fungi of the genus *Monilia*, and actually various sugars and other carbon compounds can be detected by using the specific reactions of these forms. Thus *M. tropicalis* ferments glucose, levulose, galactose, saccharose and maltose, while *M. macedonicus* ferments the first four compounds and inulin in addition, but not maltose. These authors give a table of many such differences between species. The activity in question does not include acid fermentation without production of gas.

(6) A. The effects of grafts or implants of alien tissue have in one way or another been studied for a good many years, and have some bearing on the problem before us. Whether we should regard the phenomenon of graft intolerance as biochemical or mechanical, or both combined, is as yet uncertain. The assumption is made by Loeb that they are biochemical, and indeed the work of Murphy (1913-14) lends support to this view as far as warm-blooded animals are concerned. That author showed that intolerance of a graft in the chick embryo coincides with the development of the spleen, and that, while embryonic tissue previous to this stage is tolerant of a graft, it loses its tolerance if adult spleen is grafted on to it. The only question is whether in certain other cases a mechanical factor is not also involved.

Grafting has been practised over a long period by horticulturalists, and heteroplastic grafts (grafts between different species and genera) have been made between species of different genera of plants, *e.g.* between the Quince (*Cydonia vulgaris*) and the Apple (*Pyrus malus*) ; but indiscriminate grafts of this sort are not always feasible, and relationship seems to stand for a good deal. In plant grafts the rule seems to be that " each kind of tissue is distinct in its every cell, *i.e.* there is no fusion of cells or blending of germ-plasm. . . . In each graft symbiont the two kinds of tissue maintain their identity " (Babcock and Clausen, *l.c.*, p. 374-7). On the other hand, Winkler (1910) found that there is some sort of interaction between the members of a graft-union. In his chimeras of *Solanum nigrum* and *S. lycopersicum*, it seems that a shoot arising from a periclinal graft varied in its resemblance to the parent, whose tissues were used for the inner portion of the combination, according to the number of layers of cells of the other plant which covered it. It is thus apparent that the maintenance of specific identity by a graft is not absolute. It is to be assumed that in sectorial grafts, *i.e.* when a bud arises at the point of union of the two contrasted tissues, the latter have no such effect upon each other.

Heteroplastic grafts in animals have been studied by Morgan, Loeb, Schultz, Weigl, Spemann and others. A summary of the results attained is given by Loeb (1921), who generalises as follows. Using the term " heteroreaction " (*sic !*) as meaning an adverse or hostile reaction of the tissues brought into contact, he says that in invertebrates and lower vertebrate larvæ, a " heteroreaction " is found, but it is not very pronounced. It is more pronounced in adults of lower Vertebrata, but is probably less marked in these than in Mammals.

With regard to the reactions of the tissues of closely allied species, in accordance with Loeb's summary, the grafts of embryonic tissue seem to unite and form a uniform whole, though the parts retain their specific integrity (Spemann, 1924, *Triton teniatus* and *cristatus*). The same seems to be true of larval skin grafts (Weigl, 1913), while Harrison (in Morgan, 1901, p. 185) reared grafted half-tadpoles of *Rana virescens* and *R. palustris* until past metamorphosis, each part retaining its identity.

With adult invertebrata there is apparently very great difference in the fate of transplants. Although Jost (in Morgan, 1901, p. 172) succeeded in obtaining permanent half-grafts of *Allolobophora* and *Lumbricus*, Weigl's similar experiments (*l.c.*) with *Hydra fusca* and *H. grisea* were not permanent.

The most valuable series of interspecific grafts is due to Schultz (1912-13), who, by a series of studies on Birds, Amphibia and Mammals, tested the relation between grafting and mutual fertility. Among the Amphibia used in this series, *Rana temporaria* and *arvalis* and *Bufo vulgaris* and *viridis* gave grafts which were tolerated up to 100 days, the specific colour-pattern remaining *almost* unaltered. On the other hand, grafts of *Bufo vulgaris* x *R. temporaria* only lasted some 20 days, as did those of *B. viridis* x *R. arvalis*. Rabbit x Hare grafts lasted 32 days, while Rat x Mouse were less successful. In general, Schultz says that there is a certain parallelism between mutual fertility and "graftability", though it is obvious that in individual cases discrepancies occur.

The results of such experiments may be summarised as follows:

(1) The members of a heteroplastic union retain their specific identity, even in the case of embryonic grafts.

(2) In certain instances, when very closely allied (morphologically and genetically) related forms are used, heteroplastic grafts behave as "homoiotransplants" (Loeb).

(3) The success of the union, *i.e.* its permanence, depends on the age and the evolutionary status of the organisms used. Embryonic and invertebrate tissue seems to be more tolerant of heteroplastic union than adult and vertebrate tissue.

(4) Heteroplastic grafts in animals usually behave as inert foreign substances.

(5) There is not a very close parallelism between degree of relationship and the success of grafts.

The lack of success of a graft in warm-blooded animals was assigned by Loeb (1916, p. 46) to lymphocytic action on the strength of Murphy's experiments. In his latter summary (1921) he stated, however, that in "hetero-transplants" the action of lymphocytes is relatively unimportant, though he did not state to which animals he was referring. In this place he seems to assign more importance to the injurious effect of the surrounding connective tissue.

Mention should be made of a remarkable result achieved by Spemann (1925), which has some bearing on the potentiality of the substances or forces governing the determination of "species specificity" on the one hand, and tissue- or organ-specificity on the other. This author exchanged a piece of epidermis from the gill region of *Triton cristatus* embryo with a piece of presumptive medullary fold of *Triton teniatus*. The latter, when grown on the gill area of *T. cristatus*, gave rise to gill epidermis, but this was of the *T. teniatus* pattern, not of *cristatus*, though the latter had supplied the internal environment (blood supply, etc.). The important feature of this result is that, while the organogenetic destiny was modified, the specific character of the tissue was maintained.

The remarkable capacity of transplanted tissue for maintaining its identity in an alien medium and nutrition is very well shown by Castle and Philipp's (1911) ovarian transplants and Born's *Rana temporaria* and *arvalis* grafts. In addition, it is very important to notice that functional co-operation seems to have as little effect upon species specificity. Morgan and Harrison (in Morgan, *l.c.*, p. 186) found that " when two kinds of specific tissue regenerate side by side and unite to form a single organ, there is no influence of a specific kind of one tissue on the other ".

B. A certain amount of evidence will be found in Chapter IV. which may be said to prove that the difference in distribution and habitat between allied species is determined by difference of reaction to environmental factors. It will be seen that it is by no means easy to assign such differences to single factors of the environment, particularly in the case of animals. The impression we receive from a study of distribution is that the habitat or the area of occupation is determined by a variety of factors, some of which have very little to do with the physiological constitution of members of the species. But differences of reaction and other evidence of physiological differentiation are sufficiently prominent among the causes to which we can assign difference in distribution. Whether we consider the distribution of a plant in relation to humidity, of insects according to food-plants and medium for oviposition, or of parasites according to their hosts, there is, along with other factors determining range or habitat, an important physiological factor. Availability of the host, mechanical suitability of the tissues, means of transference, etc., must count for much in determining a parasite-and-host association. But adaptation to a particular body-temperature and nutritive medium is obviously an important condition.

C. The propriety of including in this chapter the data relating to the mutual fertility and sterility of species may be called into question. Some of the causes of sterility seem to be mechanical, as in the case (p. 94) of irregularities of synapse, though we are sometimes ignorant of the fundamental disturbing cause. The causes of sterility and partial sterility, and even of incompatibility, are, however, probably rooted very largely in the physiological constitution of animals and plants, so that the bulk of the matter to be dealt with can be probably treated here.

The causes which regulate the sexual unproductiveness of any two forms are of different orders. They range from complete topographical or habitudinal isolation to physiological disharmony affecting the viability of the gametes of F_1 hybrids. Bateson has pointed out (1913, pp. 238-9) that sterility itself may be of different types, a matter to which we must return anon. There is every sort of " breeding unit " (Crew, 1925) from those founded on geographical discontinuity (with or without physiological incompatibility) to those arising from the inability to produce normally fertile hybrids. In the present chapter we are concerned with the phenomena of actual physiological incompatibility. A discussion of other modes of isolation will be found in Chapter V. The question of mechanical isolation (disparity in the copulatory apparatus) is also reserved for the latter, though it is cursorily alluded to here.

The preliminary statement of the genetic criterion (p. 12) gives us what is essentially a final answer to the suggestion that species are to be regarded as distinct " breeding units ". In the first place, we have in the capacity of producing normal healthy F_2 offspring what should at first sight be a valid test as to the status of two forms which are brought into a cross. Two forms which do not have this degree of affinity might be regarded with propriety as different species. Such a test seems about as rational and natural as one could hope to obtain. But it is now generally known that there is every degree of gradation between absolute fertility of this order and absolute sterility, so that complete fertility takes its place as one stage in such a series. Self-sterility (*v.* anon) and lack of accord in reciprocal crosses further emphasise the difficulty of obtaining a universal canon law in this matter. In the second place, let us consider the relation between the incidence of sterility and morphological differentiation.

In general there is no doubt a broad parallelism between physiological affinity and morphological status. Harrison (1916 *a*) has shown that the phylogeny of a group of moths may be elucidated by their breeding relations, which are in accord with the morphological differences. But this agreement is not always found ; we encounter, as Darwin originally pointed out, numerous cases of lack of accord. Bateson has discussed the nature and incidence of hybrid sterility (1912, chap. xi.) in some detail. Although he holds (p. 236) that " complete fertility is . . . inconsistent with actual specific difference ", and evidently is inclined to the belief that interspecific sterility is of a special order and physiologically unlike the sporadic sterility which occurs in varieties and strains of cultivated animals and plants and in certain forms of incompatibility, he allows that the incidence of sterility is singularly capricious when considered in relation to morphological divergence. Thus the culinary pea (*Pisum sativum*) and the wild Palestine race show a striking amount of sterility coupled with slight morphological differentiation (*l.c.*, p. 245). The following observations are an attempt to present some analogous cases in a systematic fashion :

(1) Actual pairing affinity is often no measure of morphological status. Harrison (1916, p. 98) cites cases in which forms which are very closely allied refuse to pair. For example, the male *Amorpha populi* was caged up with its own female and that of *Smerinthus ocellatus*, but paired with the latter ! In the same place Harrison comments on the fact that sometimes easiness of pairing and fertility are in inverse proportion.

(2) Very close morphological similarity is sometimes accompanied by sterility (Bonnier, 1924 ; Sturtevant, 1920) (*Drosophila simulans* and *melanogaster*) ; Harrison (1917) (*Poecilopsis isabellae* × *lapponaria*, etc.).

(3) Differences in the result of reciprocal crosses of different species are so well known that it is necessary to

give only one example, that of *Poecilopsis lapponaria* × *Nyssia zonaria* (Harrison, 1919), in which females were produced in excess when the male *zonaria* was used, and no females at all when the *zonaria* supplied the female.

(4) *E converso*, while some interspecific crosses may be sterile, intergeneric crosses may be fertile (*Dafila acuta* × *Anas boschas*, Bonhote, 1905) or partly fertile (Cuénot, 1921 ; Newman, 1915). Partial success may be obtained with even wider crosses (Newman, *l.c.*). The latter states that occasionally ordinal crosses may be more successful than family or generic crosses.

(5) That sterility may manifest itself at a lower level than the species of the taxonomist has been known for many years (cf. Darwin, 1859, p. 401). Self-sterility is well known among plants, but in the light of the evidence collected by Bateson its significance is still somewhat obscure. The case of *Cardamine pratensis*, studied by Correns (in Bateson, *l.c.*, p. 240) seems to show that the self-sterility is developed in classes, the members of which are incapable of fertilising themselves but are usually quite fertile with members of another class.

The concept of a breeding *unit* seems, then, to have only a partial validity, and consideration of what occurs in nature must support such a verdict. It must not be assumed that isolation (seasonal, topographical or mechanical) necessarily involves physiological incompatibility, nor, conversely, that contiguity and freedom of access involves mutual fertility. There is, however, a general parallelism between the degrees of mutual fertility and isolation. As far as isolation is concerned in the formation of a breeding unit, it will be plain from a consideration of the facts in Chapters IV. and V., and that allied species exhibit very great diversity in the extènt to which they are isolated.

The results of experimental breeding, while they reveal enough evidence to substantiate the contention of Darwin and some of his predecessors that there is no absolute parallelism between morphological differentiation and reproductive capacity, point to a general tendency in this direction. How close the parallelism is must remain for the time being uncertain until the causes of sterility are more fully known, and until we know, *e.g.*, whether the sterility and incompatibility between closely allied forms is of the same order as that between morphologically very distinct ones. Bateson (1913, p. 238 and following) has expressed the opinion that the various grades of sterility cited as evidence of the lack of any definite discontinuity between species should not be summarily treated as alike. This suggestion is of some value, though I do not anticipate that the study of sterility in its various forms will lead to the revelation of a particular type that will help us to the recognition of species.

It is a little difficult to be certain how far the results of experimental breeding are good evidence on the reproductive affinity of animals and plants in nature. If one considers the number of successful specific crosses that have been made under experimental conditions, and the large array of observations recorded in menageries, gardens, etc., by Ackermann (1896-8), Przibram (1910) for animals, and by Focke (1881) for plants, the impression received is that hybridism, whether fertile or unfertile, is of frequent occurrence. But as far as animals are concerned, artificial conditions may be held to alter the psychological and physiological condition of animals in captivity, so that as a result of captivity animals will (*e.g.*) pair with another species to which they would show repugnance in nature. Moreover, it has been suggested that in cultivation and captivity the mechanism of heredity may be modified with the consequent production of abnormal forms.

A very large number of plant hybrids are known from field observations (cf. Rolfe (1900)), and Ackermann's lists include a good many field observations. Again, it is occasionally found that forms produced as a result of hybridisation in captivity are encountered in nature (cf. Przibram (*Triton*) *l.c.*, pp. 75-7; Brainerd (in Bateson, 1909, p. 284). On the other hand, it is not seldom found that allied species display animosity and unwillingness to pair in captivity

(Diver, M.S. (*Cepea*); Detlefsen, 1914 (*Cavia*)). Captivity does not appear to minimise the traditional hostility of the Hare and Rabbit (Castle, 1925).[1] It is even on record that certain animals will not mate with their own species in captivity (Harrison, 1916). It is otherwise known that protracted domestication can modify the physiological processes of animals, so that even a short period of captivity may disorganise experimental subjects. But it does not seem likely that very far-reaching effects are produced. It is probable that on the whole animals observed in captivity behave towards the opposite sex very much as they do in nature, except perhaps after prolonged confinement in unhealthy conditions. As to the disturbance of the mechanism of heredity by captivity, this seems to me to be singularly improbable. A. Lang (1904) kept examples of *Cepea* in captivity for many years on a diet in certain cases very unlike that to which they are accustomed in nature (macaroni, carrots, lettuce, etc.) ; yet he obtained exactly the same forms which occur among the free-living animals. In any case, no proof of this contention has ever been put forward

Failure to produce a successful cross in experiment is not, however, to be taken as proof that such a cross is impossible or that it does not occur in nature. A study of the long series of crosses between varieties and species of Lepidoptera undertaken by Harrison (1914-23, *passim*) will show that success in such work depends on a very careful study of the habits and food of the animals which are used. After many preliminary failures success is ultimately attained sometimes by a change in diet or some other factor, sometimes without any apparent cause. The similar experience of MacBride (1914) should be consulted. I am also allowed, by the courtesy of Mr. A. E. Stelfox, to state that he has made successful crosses between *Cepea* (*Helix*) *hortensis* and *nemoralis*, whereas Lang (1909) only obtained very meagre results.

From the list given on page 14, in which the various stages at which sterility is established are set forth, it will be seen that the causes of sterility may be roughly classified

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[1] Female Hare killed by male Rabbit.

according to whether they take effect before or after fertilisation. The former may result from psychological repulsion or from mechanical disability (many Lepidoptera). It should be pointed out that psychological and mechanical bars to coitus may be superimposed upon physiological sterility, but a discussion of this problem is reserved for Chapter V.

A study of the ultimate causes of hybrid sterility would be beyond the scope of this work. They probably are connected with phases in cellular activity with which we are at present unacquainted. For the present we must content ourselves with the enumeration of the various disturbances in the normal cellular processes which have been recorded in these circumstances. At one time or another the following phenomena have been observed in the course of hybrid ontogeny:

A. Various disharmonies in the actual process of fertilisation, commencing with the inability of the sperm to penetrate the ovum (Lillie, 1919). In some groups at least, *e.g.* Teleosts, inability of the sperm to penetrate the ovum of another species is a rare phenomenon (cf. Lillie, *l.c.*, p. 198).

B. Failure of cleavage at various stages (Newman, 1915).

C. Cessation of or disharmony in organogenetic processes (Bonnier, 1924 ; Newman, *l.c.*).

D. Feebleness and mortality of young (Harrison, 1920 A, pp. 274, 277).

E. Disharmony in development of reproductive organs of otherwise normal F_1 (Goodspeed, 1917 A).

F. Disturbance of chromosomal mechanism (see below, p. 84).

Some of the most significant immediate causes of sterility are to be found in B and C above, and the reader is recommended to study the interesting account given by Newman (*l.c.*) of his Teleost hybrids and their development. According to this worker there occur, when fertilisation is successfully accomplished, " blocks to development " at certain developmental stages. If one of these crises is successfully surmounted, development is normal for a time until another critical phase is entered upon. These crises occur at the end of cleavage, embryo-formation, the establishment of the circulation, etc. Newman (*l.c.*, p. 470) regards the cessation of development at such " blocks " as " due to lack of co-ordination between the differentiation of the protoplasm and yolk-assimilation which fails to progress as rapidly as in normal eggs ". Thus the migration of the heart is hampered by a large mass of undigested yolk. A very much exaggerated disharmony in development is seen in the *Drosophila melanogaster* and *simulans* hybrids. In these forms Bonnier (*l.c.*) found that certain organs remained in a larval condition when others had completely metamorphosed. These periodic crises are recorded by Harrison (1916, p. 100) in his Lepidopteran crosses, in which the failure of development is more frequent at the egg-stage and first larval instar. Comparing such cases with those indicated in A, in which the sperm and egg seem to have an immediate toxic effect on each other which inhibits further development, it is uncertain whether in B and C we have a delayed toxic effect, or whether, as Newman would suggest, the material from each gamete maintains its own rate of development, and death is the result of a process of actual disintegration resulting from these rates not being synchronised.

The classical researches of Godlewski and Loeb on artificial fertilisation have shown that spermatozoa which cannot normally penetrate the ova of different species may be enabled to do so, *e.g.* by rendering more alkaline the sea water in which the eggs of Echinoderms are fertilised. This process can apparently be regarded as a neutralisation of the mutual toxicity of the egg and sperm used.

The adverse effect of hybridism on the germ cells of otherwise normal F_1 organisms is a very difficult matter to explain. It is hard to see why, when the rest of the organism may be normal and healthy, the germ-cells alone are singled out by developmental disharmony. At present we know very little as to the actual nature of the disturbance in the gonads of sterile hybrids. Bonnier (1924) found that the ovary actually degenerates in the oogonial stage, and Sturtevant (1920, p. 498) found no sperm formed in the testis. On the other hand, Harrison (1916, pp. 114-15) found the primary genitalia microscopically normal.

Among the various disharmonies observed in hybrid development are chromosomal irregularities. These include actual disorganisation of the nuclear mechanism (abnormalities of synapsis (Smith and Thomas, 1914); failure to pair (Harrison and Doncaster, 1914; Federley, 1913), or reduplication of number (Gates, 1921). Whether in all such cases we are to regard the actual abnormalities as *causes* of sterility is doubtful. Bonnier (1924) found the chromosomal phenomena of the sterile hybrids of *Drosophila* to be normal. Actual reduplication is apparently not responsible for sterility, as Harrison and Blackburn (1921) find that the hybrid *Rosa Wilsoni*, which has doubled the original complement, is fertile. The crucial question appears to be whether the number attained is balanced or unbalanced.

A curious example of what we may regard as the selective effect of sterility is recorded by East (1916). He states that in his *Nicotiana* crosses the corolla shows no sign of that increase in size and vigour which is characteristic of the vegetative parts of these hybrids. If other facts of a like nature are forthcoming, they would seem to suggest that not only the germ cells, but also the accessory sexual structures, may be subject to the special selective disturbance induced by crossing.

The cause of the beneficial result of the meeting of differently constituted germ plasm noted by workers from early times has been extensively studied, and two main views have been advanced. It should be noted that East and Jones (1919) refute the suggestion that hybrid vigour is to be explained on the ground that such forms expend less energy on seed formation. They point out the obvious fact that many flourishing hybrids " manifest even greater ability (than their parents) to produce seed ".

It has been suggested that " heterosis " (hybrid vigour) is due to either a physiological stimulus, or is the combination of the appropriate factors for vigour which are brought in by different parents (East and Jones, *l.c.*, ch. viii., *passim*). A full investigation of the rate of cell-division is obviously desirable before we can reject the first hypothesis. It is worth while noting that Roberts (1912) recorded an increase in the size of seed in crosses, and that Harrison (1916*b*) noted increase in size of cells in Lepidopteran hybrids. On the other hand, East, Jones and Emerson produce evidence (*l.c.*, p. 183) which gives a satisfactory explanation of vigour from the other point of view. We should not lose sight of the fact that the well-being observed in hybrids need not necessarily have the same cause in all cases.

In the preceding pages we have seen that there is a general tendency to differentiation in the physiological and biochemical properties of organisms, which may not exhibit a specificity exactly parallel to morphological distinctions, but nevertheless lends some support to the doctrine of " physiological specificity ". It will be as well to mention some cases in which such differentiation is positively absent.

It has already been said (p. 67) that the hæmatin component of hæmoglobin is uniform in all the Vertebrata examined. Fowler and Malakhandar (1923) have examined the amount of CaCo present in the shells of certain species of Mollusca and found that it is very much the same in different species ; while Schmalck (1901) has, with data somewhat inadequately presented, demonstrated the same fact for Sulphate of Lime and Phosphoric Acid. Willstater (in Blackman, 1921) has shown that the chloroplasts of various plants are identical in composition. Loeb (1921) has recorded an absence of " species differential " in placenta extracts, and in the growth substances which determine the development of the lens and metamorphosis in Amphibia. The latter substances are stated by him to be of a common lipoid nature. It is finally pertinent to add that closely allied species may sometimes show a very pronounced difference in excess of the evolutionary relationship, as, for example, the presence of hæmoglobin in *Planorbis corneus* and its absence in the other species of that genus. A similarly capricious distribution is seen in the products of metabolism of certain Fungi. According to Ramsbottom (1923, pp. 56-7) the poisonous properties of various members of this group are not specifically differentiated. In certain cases, however, such distinction does occur, as in *Amanita phalloides* and *muscaria*, from which two substances, *phallin* and *muscarin*, producing different clinical symptoms if eaten by human beings, have been obtained. Extracts from *A. phalloides* differ from *muscarin* in the degree of severity of the symptoms produced. But more usually we find no such distinctions, and the incidence of toxicity in this group seems to be quite irregular.

In considering this class of phenomena, we must bear in mind an obvious fact to which reference has been already made. It does not follow that failure to show a differential reaction in one set of circumstances is a proof of an all-round similarity of constitution. As already stated, Wells (1925) has shown that negative immunity-reactions are obtained from the water and salts, and probably from the carbohydrates of animal and plant tissues. The fact that Reichert (*l.c.*) obtained specific reaction by other means from the starches of plants is a sufficient proof that a single method of testing for specificity is not sufficient. We must therefore refrain from concluding that a given property or activity of animal or plant tissues is lacking in specific differential until all its more important reactions have been ascertained.

There are two main questions which suggest themselves as a means of summarising the data given in this chapter. In the first place, we are entitled to know if the functions of intimate properties of living beings are differentiated to the same degree as their structure. If such differentiation occurs, it is of importance to know whether it is a property of any particular constituent of the living substance.

To these questions it is obvious that we can reply at present only in a tentative fashion. The answer is, the first is perhaps the easier. It seems that the living substance and its constituents, and the mode and products of its activity, do show a differentiation which in a broad sense marches with structural differences. The pace is not, however, uniform. Physiological differentiation of the type herein examined seems at present to be more erratic and less definitely canalised than that of structure. It is true that the inheritance of certain physiological differences (*senso stricto*) on Mendelian lines has been proved, *e.g.* by Pearl and Bartlett (1911) and Learmonth (1920). But, as far as one can speak of such attributes collectively, they seem to be erratic in the sense that individual fluctuations are more marked, and they are less subject to clear-cut differentiation. Nevertheless an approximation of the two modes is tolerably close, and one receives the impression that the more this subject is explored the closer the approximation will become. It is almost impossible to answer the second question with confidence. The proteids seem, as Loeb and Wells state, to be subject to the most acute differentiation, though I doubt whether they are the " bearers of specificity " as Loeb thinks (1916, p. 61), if indeed that phrase has any real significance. Evidence of differentiation in other substances is not, however, very copious, and in some it is apparently absent.

It remains for me to return for a moment to the work of Spemann, noticed on an earlier page (p. 75). It will be remembered that, if a transplant is tolerated and does not provoke a " hetero-reaction " in the stock, it maintains its specific character unimpaired. Spemann's achievement has been to show that up to a certain stage in development, the functional destiny of transplanted tissue is modified, while its specific character remains unchanged. The *Triton teniatus* medullary fold becomes gill-tissue when grafted on to *T. cristatus* gill, but it remains *teniatus* in colour (Spemann, *l.c.*, Fig. 9). Although they are both exposed alike to an alien medium, the function of the transplanted cells is altered by the latter, but the colour is unchanged. From the work of Koppányi (cited by Przibram, 1926, p. 322), it would seem that colour in grafts does not always resist the pigment-bearing ferments of the stock. This branch of experimental work is obviously not sufficiently advanced to allow us to speak with any certainty; but it is plain that if it is extensively carried out it should supply very valuable clues as to which parts or properties of the organism retain their specific identity with the greatest tenacity.

CHAPTER IV

THE DISTRIBUTION OF ALLIED SPECIES

OUR object in this chapter is first to ascertain whether the areas or the habitats occupied by allied species are in general identical, overlapping or totally distinct, and then to ascertain how interspecific differences in distribution are brought about, viz. whether they are based on differences of (1) adaptation, or (2) fortuitous dispersal conditioned only by time and the availability of habitats and areas of occupation. Before undertaking this inquiry, we ought to state how far the distribution of taxonomic species can be used in evolutionary discussions. The facts presented in the first two chapters must forcibly remind us that specific distinction is not always to be taken at its face value.

Inferences based on the facts of distribution are liable to error or uncertainty, as a result of the arbitrary nature of the species-concept and the bias of the individual systematist. One naturalist will multiply species by seizing on any difference (" splitting "), while another will unite a large number of forms under one name (" lumping "). The vicissitudes of forms treated in this manner must inevitably produce scepticism as to the utility of generalisations erected upon such data. I may state without comment that while Gulick, in his celebrated studies of the effect of isolation on the Achatinellidae of the Sandwich Islands (1905), recognised some 200 species, Pilsbry, Hyatt and Cook in their recent work (1912) reduced this total to forty-three!

Such divergence of opinion must warn us to hesitate before accepting, *e.g.*, generalisations on the effects of isolation. Thus an insular form more or less distinct from its mainland relatives may be regarded by one systematist as a species, or by another worker as a variety. The use of the specific status enlarges our idea of the effects of isolation, while the varietal status may give too low an estimate. In such circumstances we obviously should try to think not in terms of rigid categories, but of the number and degree of divergence of the differentiated characters ; and needless to say we should refrain from utilising data concerning the distribution of species described from a few specimens only.

As regards " species " that are held to be environmental forms of other species, I think we should take up this inquiry without *parti pris*. For the time being at least we should suspend judgement as to the causes of heritable variation, and consider simply what are the facts of structural differentiation in relation to distribution.

We have already seen (p. 58) that morphologically identical forms may have different habitats. Thus a single " species " may have a number of different food-plants, or, if it is a parasite, it may occupy hosts belonging to different genera or families. I have pointed out that it must not be always inferred that such differences imply permanent physiological differentiations. If such differentiation is proved, however, we are obviously confronted with two mutually contradictory criteria—morphological similarity and bionomic or physiological dissimilarity. Actually the criteria cannot be formally reconciled ; though in practice we usually employ the structural criterion as more readily fixed.

If our data thus seem to be compromised by the arbitrary nature of the species-concept, it may very well appear that we can draw no safe inferences from them. On the whole, however, the groups of animals and plants recognised as species do represent divergent tendencies. We may, it is true, err in attributing hereditary stability to one form, or we may exaggerate the differences between two forms by calling them species ; but in the main our task is to relate structural and other modes of divergence to differences in distribution, and a description of specific differences of this kind must give us some general index of that relationship.

It is neither easy nor desirable to discuss the distribution of allied species in space as an isolated and self-contained problem. As long as it is regarded as a mere enumeration of areas occupied, it can be satisfactorily detached from the rest of descriptive biology and studied *in vacuo*. As soon as we begin to consider the distribution of organisms more intimately, to look to the *habitat* rather than to the area occupied, we are forced to depart from the simpler method of approach. Still more difficult is it to confine the subject when we come to consider the causes of differential distribution, for we are driven into other fields of inquiry—to the physiological differentiation of species, to the study of habits, heredity and reproduction.

The exhaustive study of habitats is one of the most neglected aspects of Zoology. The historical generalisations on the distribution of animals, founded as they are very largely on that of vertebrates, are mainly geographical. But since the beginning of the present century there has been a welcome tendency to adopt the technique of Botanical Ecology, and to consider the ecological "niche" rather than the area.[1]

At the present time we are far from possessing accurate data as to the precise limits of the distributional areas and habitats even of our well-known species. This is particularly true of some marine invertebrates. The southern range in the Atlantic of many Northern or Mediterranean species of molluscs, and the limits of the widely spread "Indo-Pacific" species are only vaguely known. The "provinces" of the earlier zoo-geographers are often found to be in need of re-definition; and the extent to which great oceanic "divides" like that between the Benguela and Mozambique

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[1] An admittedly slight acquaintance with animal ecology has left me very sceptical as to the propriety of treating the *habitats* of animals (cf. Richards and Robson, 1927, p. 1114) in the same way as those of plants. I anticipate much enlightenment and a fresh orientation of our ideas on this subject from a book on animal ecology by Mr. C. S. Elton now in the Press.

currents off Cape Agulhas separate distinct faunas is only known in a very general fashion. Speaking of a group of marine animals which I have had occasion to study in detail, namely the Cephalopoda, I have to confess that the knowledge at present available, even on the depth at which these animals are found, rests largely on the unsatisfactory catches of open nets, which give no exact clue to the depths at which an organism is found (Robson, 1926). It is likely that this criticism is valid for other groups. With regard to parasites, our knowledge is more exact ; but it is often true that only the name of the host is given, and no reference is made to the part or parts of the latter occupied by a parasite. In spite of some outstanding exceptions, the data of geographical distribution are actually valueless materials for evolutionary theory. We require a large amount of information as to the exact habitat or range of habitats, habits, food, enemies, associated plants and animals, etc., which alone can enable us to discuss the problems of isolation and adaptation. It is, of course, a commonplace among systematists and geneticists that the relations of closely allied forms can only be determined by reference to a large number of individuals, and intensive collecting in the field and the analytical treatment of material thus obtained is happily in practice to-day. But we have not as yet made up our deficit in this respect, and, in spite of intensive collecting in many groups, much of our knowledge as to distribution and the theories that are based thereon rest upon very inadequate foundations.

The necessity for intensive collecting is, as I have said, generally recognised to-day ; but it may not be fully realised how necessary it is for our theories of distribution and isolation. A single example should make this plain. In 1913 the late Captain Barrett-Hamilton and Mr. M. Hinton described as a new species a shrew (*Sorex grantii*) from the island of Islay in the Inner Hebrides. In 1922, Mr. I. Montagu (1922) obtained a fresh supply from Islay as the result of a more intensive search. On the strength of this material he succeeded in linking up *Sorex grantii* with the British (mainland) and continental *Sorex araneus*, and felt compelled as a consequence to reduce *S. grantii* to a variety of the latter. It need not concern us unduly to consider whether Mr. Montagu's verdict and opinion were correct. The main issue is that more extensive collecting revealed the presence of other forms on the island which are less distinct from the mainland form, and thus reduced the amount of difference between the latter and the insular race.

The intensive study of distribution is still more necessary when we deal with local and geographical races. Any naturalist with experience in collecting invertebrates will testify to the care and patience necessary in order to obtain a fair sample of a population. Places from which collections are made in one season or in one set of climatic conditions, or from which only the largest or best-looking examples are chosen, may easily yield deceptive results.

Before we attempt to discuss the causes of differential distribution, I think we should indicate in a broad way the general facts as to the actual distribution of allied species. The question which we must seek to answer is at the last resort—do allied species tend to inhabit different areas or habitats ?

It is very important to bear in mind the distinction between difference of area and difference of habitat. Two forms which inhabit the same area may have such differences in habitat as to be quite distinct in their actual distribution. Ortmann (1905, p. 91) has shown that more or less closely allied species of Crayfish (*Cambarus*) which occupy the same, or nearly the same territory, may have different habitats. Thus *C. virilis* inhabits running water, while *C. immunis* is a ditch- or pond-form. *C. diogenes* is largely restricted to plains, while *C. monongolensis* is found in hill country. Ford (1923) has shown that on the sea-bottom just outside Plymouth Sound, *Tellina fabula* and *T. crassa*, two Lamellibranch molluscs, inhabit soils of different grades of fineness ; while similar facts are recorded by Hewitt (1914, pp. 5-6) and Broome (1907, p. 296) for Spiders and Mammals respectively. It is not likely that such differentiation will be clearly marked as a rule. Such ecological separation may coincide with purely geographical separation, when there is a " succession " of ecological conditions over a wide area. Thus *Cardium edule*, the Common Cockle, is tolerant of low salinity, while *C. exiguum* and *fasciatum* do not thrive in water of under 25 p.m. There is therefore in most estuaries a discernible topographical difference in the distribution of these forms, which corresponds with differences in salinity ; but there is also very frequently a considerable amount of overlap between the species which occupy different places in such a "gradient". Differences of habitat are not always easy to establish, especially in the case of small invertebrate animals. If the latter are taken in a net or " grab " or in tangled masses of plants from a pond, it is by no means easy to decide if such animals are living, for example, on the same plants. For this reason many of our records for animals are of very little value for discussions of this sort. Another circumstance for which allowance must be made is that the habitat of a species may not be the same over the whole of its range. Thus the small water-snail, *Paludestrina jenkinsi*, seems to be very largely restricted to fresh water in this country, while its continental distribution is, as far as we know at present, estuarine (Robson, 1923, and MS.). Another and more interesting case is provided by Mr. E. Ford's recent demonstration (1923) that off Plymouth the species studied by Petersen in his animal communities of Danish waters do not always form part of the communities that Petersen defined (cf., too, Carpenter (1927, p. 51)).

The distribution of allied species has received in the past a full measure of attention chiefly in connection with inquiries as to the effect of isolation. As far as animals are concerned, the observations mainly relate to vertebrates. The subject is discussed in an interesting study by Leavitt (1907), who makes the important point that the botanical and zoological evidence is at variance. The studies of M. Wagner, Merriam and Jordan, to which we may add the evidence of Stone (1903), Steere (1894) and Ruthven (1908), all tend to show that directly related forms usually occupy distinct but adjacent territories. On the other hand, an intensive study of the orchids of the United States, supported by other studies on *Hepaticae*, *Equisetales*, *Algae*, *Crategus*, etc., led Leavitt to another conclusion. According to this author, among plants, closely allied species and varieties are not thus sharply delimited in their areas of distribution, but may be very frequently found together, or may show a large amount of overlap.

When, in addition to geographical distribution, habitat preference is taken into account and many groups of organisms are considered, it seems that no universal formula can be framed to cover the facts of distribution as far as allied species are concerned. Each group has to be considered on its own merits, and the special mode of life and method of feeding and reproduction borne in mind. I speak with considerable hesitation about plants, but it would appear that closely allied forms in general occupy overlapping areas. Dr. J. Willis suggests that amount of overlap depends on the size of area. Such areas may in the present state of our knowledge be purely geographical, as in the case of the species of *Talauma* and *Michelia* among the Magnolias (Goode, 1925). Others again are delimited more or less by ecological conditions, as in the succession of lowland and Alpine species of *Draba*, *Viola* and *Pinus* (Warming, *l.c.*, pp. 251 and 312-14); and abrupt differences of ecological conditions may produce discontinuous distribution, *e.g.* when there is a marked difference of geological formation between two areas. I think the same general conclusion is to be made concerning invertebrate animals. When due allowance is made for the differences in habit and food already alluded to, it seems that among such animals allied species usually have a certain measure of overlap in their distribution. Enough examples might be found to establish a numerous array of exceptions. Thus Hewitt (1918) found many closely allied species of spiders occupying adjacent, but distinct areas. The case of the North American Crayfish has already been discussed, and numerous instances could be given of distinct host-specificity among parasites (see p. 104). These examples, however, do not weaken the general impression of a very considerable amount of overlap in the range of allied species. It is scarcely possible to cite the array of evidence on which this generalisation is based, and the arguments whether in a given case topographical coincidence is accompanied by habitudinal difference would occupy a large amount of space. A few examples from a very large number of cases of habitudinal overlap or coincidence may be given. They relate to Tiger Beetles (*Cincidela*) noted by Hamilton (1925), Water Bugs recorded by Poisson (1924), *Pisidium* (Alkins, 1924), land and water snails (Robson, MS.), Spiders (Dahl, 1921), and Bees (Richards, MS.). Reference has already been made to the work of Petersen on animal communities in Danish waters. This author remarks that " closely related species, especially those of the same genus, are scarcely ever found living in one and the same area of a given water ; they may meet and fight out their war on a frontier line. . . . Each (species) has its own region, its own community " (1915). The extent to which this statement is true may be tested by Mr. Ford's recent work on communities of the sea-bottom off Plymouth (1923). From the table given by this author (p. 169) of the organisms found in two different types of bottom, we obtain the following result. Fifteen genera are represented by more than one species, and of these the different species live on different bottoms in seven cases, on the same bottom in four cases, and overlap between the two contrasted types of soil occurs in four cases. The number of genera is low ; but for what it is worth we may say that there is something like equality in numbers between the species with separate habitats and those with the same or overlapping habitats.

Among vertebrates instances could be readily found of coincident or overlapping distribution in all the classes. I am inclined to believe, however, that topographical and habitudinal segregation is much more definite among close allies in this phylum, at least among Reptiles, Birds and Mammals. In the first two classes instances of the isolation of allied species from one another are to be very readily found, while in Birds the geographical segregation of varieties and " races " is by no means uncommon.

It seems, then, that allied species may be found occupying the same habitat or territory, spatially separated or overlapping one another. This conclusion may at least serve to remind us that in certain groups spatial isolation is not of such general occurrence as some students would have us believe. We should also bear in mind that, as far as isolation is concerned, forms which live in the same habitat may be debarred from producing fertile offspring by other causes.

As a preliminary to a review of the causes of differential distribution, it will be convenient to examine two examples of this phenomenon.

From the observations of Mr. E. Ford on the animals of the sea-bottom off Plymouth, it is apparent that the two small bivalve molluscs, *Montacuta bidentata* and *substriata*, live on different soils, one on a coarse, the other on a fine sandy bottom. It is possible that Time can be excluded as a factor in determining the difference in distribution, as the two species are found in the same area but occur on different patches of bottom. Here, reaction to environment might be the limiting factor. But how are we to look on the origin of the difference ? Does *Montacuta substriata* possess such a physiological and structural constitution that it can only live on a coarse soil ? Is the relation in this case based on method of locomotion or some other cause ? Or does it depend upon some specific article of diet found only on such soil, or upon some relationship with the other animals living on that soil ? Or is the association of this mollusc with that particular soil fortuitous ? Was the coarser soil a " niche " in the economy of the sea-bottom which was untenanted by animals of the *Montacuta* sort and the only available one left for *M. substriata* as it evolved, so that, while it could easily have lived on the finer soil, it had no alternative but to colonise the other ?

It seems, then, that we can explain the occupation of different habitats by these allied species in two ways.

Such species may occupy different places in the economy of Nature, either because they can only live in the presence of factors exclusively found in those places, or else in the absence of such strict ecological adaptation, a species may settle in a given habitat or area because it happens for the time being to be unoccupied.

Let us now consider another case of differential distribution, this time one of different geographical areas. The typical form of the wall-lizard (*Lacerta muralis*) is found at the present time all through Central Europe from the Channel Islands eastwards to the limits of the Danube system, in North and Central Spain, Italy and the Balkan Peninsula (Boulenger, 1920, p. 175). Its local and geographical races expand its distribution far wider, *e.g.* to Portugal, North Africa, Transcaucasia and Persia. On the other hand, *Lacerta peloponnesiaca* is found only in the Morea, with a possible representation in Crete (Boulenger, *l.c.*, p. 162). As in the last example, the difference in distribution in this case may be due to differences in constitution so that, e.g. *Lacerta peloponnesiaca* can only live in the ecological conditions characteristic of the Morea. On the other hand, the present distribution may not be an index of the differing constitutions of the two species. Given time and the appropriate means of dispersal, *Lacerta peloponnesiaca* may eventually spread further afield and occupy the same area as *L. muralis*. Or it may be a species in course of extinction and ultimately contract its area of dispersal to a more limited compass. If the size of the area occupied by a species is a function of the age of the latter, we do not thus obtain an explanation of the occupation of different or of overlapping areas, but we are put on our guard against assuming that differences in the area occupied must imply differences of adaptation.

The environment in which any plant or animal lives is composed of very many factors which may be mutually dependent and operative in determining the range of an organism. These factors may be found analysed and classified in any book on animal and plant ecology (*e.g.* Shelford, 1913; Warming, *l.c.*; Dahl, 1923; Thienemann, 1926). They may be chemical (*e.g.* the amount of oxygen, carbon dioxide, nitrogen, etc.), physical (*e.g.* degrees or amount of atmospheric moisture, temperature, light, viscosity of water, pressure, etc.), physiographical (currents, depth, slope of land and direction of facing) and edaphic (*e.g.* nature of soil and its dryness or moisture). They include the amount and kind of food, enemies, materials for nesting or making abodes.

These factors may regulate the lives of animals and plants either directly as they affect the general or special metabolism of the organism, or indirectly as they may control reproduction (time and duration of breeding season, site of nesting or oviposition, etc.).

Lastly, we should include the general interdependence of all organisms, not only as food but also in special ways, such as the availability of hosts for parasites, intervention of fertilising agents, opportunities for commensalism, etc. (" Biotic factors "). Shelford (1913, p. 32) has defined ecology as " that branch of general physiology which deals with organisms as a whole . . . as distinct from the more special physiology of organs". This orientation of ecology towards physiology can be perhaps easily justified; but, in the sum total of factors that may determine the habitat or range of a plant or animal, it is doubtful whether the strictly physiological factors are more important than the biotic.

In any attempt to decide to what extent allied species are controlled in their distribution by different reactions to external factors, there are some limiting circumstances which must be stated as a preliminary:

A. As stated previously, topographical coincidence of two species does not necessarily imply identity of habitat.

B. Size of area has no constant relation to strictness of habitat preference. A species may have a very wide range, but at the same time it may be adapted to a very limited environment. Many widely ranging marine animals may keep within narrow limits of temperature, salinity, etc., while others of more limited range may have a wider toleration of temperature and salinity.

C. The size of the area occupied by a species and the extent to which it tolerates environmental conditions has no direct bearing on the distinctness of its area or habitat from the habitats of other species, though usually a widely tolerant or widely ranging form will tend to overlap other species.

D. A species may be restricted to a habitat or an area by adaptation to a single factor or a general adaptation to several. Actually many external factors must be inter-dependent (*e.g.* salinity, density and deposition, cf. Robson, 1925).

E. As many factors may obviously be concerned in the determination of habitat, it must not be assumed that because a species has a limited range *vis-à-vis* a given factor, it is necessarily limited by that factor alone.

F. Experiment or the proof of invariable correlation between a given factor or factors and the occurrence of a species are our only means of determining what the limiting factor or factors may be in any given case.

Evidence was presented in Chapter III. as to differences in metabolism and other vital activities between allied species. Some of this evidence might lead us to anticipate such differences in the mode of reaction to external stimuli as may be likely to cause differences in distribution. It must nevertheless be confessed that at the present time it is not easy to find much data bearing on the latter point. A very considerable body of evidence is available as to differences of habitat, in which chemical and physical factors may be assumed to play a large part (*i.e.* occupation of areas of different salinity and hydrogen ion concentration) ; but for the moment we are concerned with the experimental proof that different species do actually react differently to single factors. Such differences are known to occur between species of different genera and orders, but, as usual, specific differences within the same genus are not frequently dealt with, and in some instances they have to be rejected as evidence on account of deficiencies of method. For example, when differences of reaction between allied species are recorded they are frequently not accompanied by information concerning the size and age of the individuals tested, their sex and reproductive condition, and their general physiological standard. All of these factors ought to be evaluated before we can discuss inter-specific differences.

Though satisfactory evidence of distinctions of this sort is available, it is, however, sometimes found that allied species have identical reactions. It would be premature to attempt to decide whether difference or similarity of reaction is more common. In any case I do not think it at all likely that differences of susceptibility to single environmental factors are likely to be the basis of many distributional differences.

We have already seen that there is a well-marked tendency for allied species to occupy different or overlapping habitats. It will be of service now to define such habitats a little more strictly, so that we may gain some insight into the factors by which species of plants and animals may be governed in their choice of habitat. It must not be forgotten, however, that the occupation by a species of a habitat differing from another habitat in a single primary factor does not prove that the distribution of the species in question is directly determined by the factor in question unless the species is known to occupy the said habitat invariably and other circumstances governing distribution can be evaluated. For example, if a certain species of fish is always found in running water, it may not be directly influenced by the pressure of the water in its choice of such a habitat, but by some type of food or certain conditions of oxygenation characteristic of running water. If we can ultimately evaluate all the secondary factors, we are entitled to say that the actual speed of the stream is the basis of such a preference. I am not, however, familiar with any refined analysis of this kind, and the following data are of general habitat-preference alone. As far as strictness of the latter is concerned, *i.e.* the extent to which species of the same genus occur in different habitats, and may be held to be rigidly isolated by differences of preference, it was seen above (p. 96) that distributional overlap is very common, and it is likely that, just as species are morphologically diverse in their composition, so they may contain strains differing in their adaptability to the factors of their environment.

Among plants, the succession of species is sometimes correlated with a gradient in the intensity of a single factor. Thus Clements (1916, p. 93) has shown a difference in the succession of *Pinus murrayana* and *P. ponderosa* accompanied by differences in the intensity of light. Differences in the distribution of other plant species are recorded in relation to geological formations. Thus Kerner (in Warming, *l.c.*, p. 57) notes that there is a wide difference in the plants which occupy limeless slate and limestone. *Anemone alpina*, *Juncus monanthos* and *Primula amicula* are " calcicolous " ; *A. sulphurea*, *J. trifidus*, and *P. villosa* are " non-calcicolous " ; *Androsace haussmanni* is restricted to dolomitic soils, *A. glacialis* is " non-dolomitic ". Warming (*l.c.*) gives similar differences in the occurrence of related species according to the presence of zinc and serpentine, and of silica as opposed to calcium. The copious literature of plant-succession should be consulted, in which the dominants of different ecological units are often shown to be different species of the same genus (cf. Clements, *l.c.*, p. 234). But in all these instances it is not easy to associate the observed differences in distribution with a definite single factor. Even when we are dealing with the " gradient " of a single physical factor such as light, it is by no means certain that differences in the intensity of the latter are the direct cause of distributional differences.

Among animals related species may often be found to occupy different parts of an environmental gradient. Some of the best-known instances of this occur among marine animals. Murray and Hjort (1912) give many examples of such differences in relation to depth (e.g. *Cyclothone microdon* and *signata*, p. 621 ; *Acanthephyra multispina* and *purpurea* ; species of *Euchaeta*, p. 639). Johansen

(1915, pp. 443-4), in his study of succession in Rander's Fjord, showed that in many cases species of the same genus are regularly distributed at different parts of the salinity gradient. I have already noticed the occupation of different bottom-soils (Ford, *l.c.*) and of running and still water (Ortman). Boycott (1919, p. 14), from a careful analysis of the population of fresh-water mollusca of a limited area, found that *Limnea pereger* occurs in all the ponds and streams which were surveyed, and *L. auricularia* is absent from " closed " and running ponds. *Planorbis nautileus* and *spirorbis* were found in closed ponds only, *P. corneus* in running ponds and streams only, and *P. complanatus* in all *loci*. Among land-snails *Pyramidula rotundata* is ubiquitous, and *P. rupestris* occurs only in limestone areas ; *Agriolimax agrestis* again is ubiquitous, while *A. levis* is found only in damp and marshy places (Boycott, *l.c.*, p. 237); (Stelfox, 1911). Species of insects are very often strictly delimited by their food plants. Thus *Cecidomya destructor* occurs on wheat, *C. avenae* on oats (Cuénot, 1921, p. 411), and the plant association serves to delimit the distribution of other animals, examples of which are given by Shelford (*l.c.*). *Epeira gigas*, for example, occurs in Tamarach undergrowth and Willow thickets, while *E. foliata* occurs in the former alone (pp. 206-8).[1]

The periodic fluctuations in the distribution of marine organisms is sometimes correlated with specific changes in physical conditions. Thus Hardy (1923) associates the intermittent appearance of the Pteropod *Limacina lesueuri* in northern waters to recurrent influxes of Atlantic water, and Bardarsson (1910) invokes the marked changes in temperature known to occur off the coast of Iceland at the present time to account for the change in the distribution of *Littorina* in the raised beaches of that country. Indeed it is the practice of geologists and students of animal life in post-Pliocene times to

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[1] Important data on the distribution of various marine invertebrata according to soil are to be found in a work by Captain F. M. Davis, which was received too late for adequate treatment herein (Ministry of Agriculture and Fisheries, *Fishery Investigations*, Ser. II. vol. viii. No. 4, 1925).

diagnose changes of climate by the occurrence of " Northern " and " Southern " species in deposits. I am a little doubtful whether the practice is a sound one, for it rests on the assumption that the reactions of species remain unchanged over long periods of time.

Differences of habitat are plentifully found among parasitic animals, though allied species may also be found to have similar hosts. Such differences may relate to (*a*) the organ or part occupied, or (*b*) the host.

(*a*) Of the first kind of difference we have a notable example in the distribution of *Pediculus capitis* and *P. corporis humani*. *Necator suillus*[1] is found more commonly in the ileum, and *N. Americanus* in the duodenum and jejunum (Cort, 1925). *Entamoeba coli* lives freely in the large intestine, while *E. histolytica* is usually found in the intestinal wall (Dobell and O'Connor, 1921). Some species of *Eulima* (Gastropoda) are ectoparasitic on Holothurians, while others are endoparasitic.

(*b*) The term " specificity " is used by students of parasitic organisms to indicate the occupation by a parasite of a limited range of host-species. A parasitic species may be restricted to a single host-species or it may inhabit several, " specificity " being, as Caullery has indicated, essentially relative and manifested in extremely variable degrees. Baylis (1924, p. 13) has pointed out that in some groups it is more strictly manifested than in others, citing the Gregarines, Mallophaga and Epicarida as examples of strict, *i.e.* limited, " specificity ".

The question we shall consider here is not whether a given parasite occupies one or more hosts as indicated above, but whether different species of the same genus, when parasitic, occupy different hosts. How common an occurrence this is I am unable to say. Examples are easy to find of the occupation of the same host by different allied species. Thus Baylis (*l.c.*, p. 20) records *Ancylostoma braziliense* and *caninum* from the Dog and Cat, and Nuttal

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[1] Since Cort's paper was published some doubt has been expressed as to the structural distinctness of these species.

(1911, p. 48) lists Argas *reflexus* and *persicus* from Birds and Man. Many authors allude to the host under a general term " Cattle ", " Birds ", etc., without distinguishing the species. The following are obvious cases of differentiation of specific habitat. *Argas vespertilionis* occurs only in Bats, *A. reflexus* and *persicus*, as stated above, in Birds and Man (Nuttal, *l.c.*). Of nine species of *Ornithodorus* the distributions is as follows :

O. savignyi	Man, camel, horse.
moubata	Man, dogs, pigs.
turicata	Man, pigs, cattle, llama, horse.
talaje	Man.
,, *capensis*	Birds.
pavimentosus	Man.
tholozani	Fowls and camels.
lahorensis	Sheep.
megnini	Man, horse, ass, ox.

From this list it will be seen that there is a fairly clear differential tendency. The same host species may be occupied by several parasitic species ; but the total range of each parasite *as known at present* differs, except in the case of *O. talaje* and *pavimentosus*. It is necessary to qualify this statement, as it is very unlikely that we know the complete range of hosts at present.

Other examples may be given of a similar kind illustrating differences in habitat between parasitic species belonging to the same genus ; and from a perusal of Stiles and Hassall's " Catalogue " (1920), I am led to infer that on the whole the parasitic species of a given genus tend quite definitely to occupy a different range of hosts, though overlapping series are frequent and identity of hosts is sometimes recorded.

The breeding habitat has been sometimes shown either to be determined by definite external factors, as in the case of the Tiger Beetles, *Cincidela* (Shelford, 1908), or to be represented by a fixed characteristic habitat. Kemp (1914) gives a clear case of the latter in describing the breeding-migrations of the Prawns, *Palemon malcolmsi* and *lamarrei* (1915, p. 265 and following), while Cuénot (1917) has shown that similar differences may occur between races or varieties of the Cuttlefish, *Sepia*.[1] This matter will be more fully discussed in the next chapter.

When we state that some species are more tolerant of a wide range of environmental conditions, or have a more extensive geographical distribution, we may, in the light of what has been said concerning taxonomic species, be treating as referable to the same species forms which are actually distinct. For example, the Cephalopod, *Todaropsis eblanae*, commonly found in the Mediterranean and N. Atlantic, has been recorded by myself in the waters off the Cape of Good Hope. The South African form is, however, distinguished from the Northern form in sundry features, the taxonomic significance of which is still uncertain, and we await a more complete study of the variation of this form before we can assert that the Cape form is actually identical with the Northern. It is obvious that no hard and fast line can be drawn between forms with a "limited" habitat-preference and "widely tolerant" ones. It is only necessary to repeat the previous warning that width of range must not be assumed to imply wide toleration of conditions unless the habitat is also known to be diverse as well. It has already been pointed out (Richards and Robson, 1926) that probably no two habitats in widely separated geographical areas can be exactly alike, particularly in the biotic (see p. 99) factors as opposed to the physical; but they may often be similar enough as to render any divergence attributable to them to be unimportant.

The numerical incidence of wide as opposed to narrow toleration has not, as far as I am aware, been systematically explored. Warming (*l.c.*, p. 66) considers that most plant species are confined to soil that has quite definite physical and chemical peculiarities. More positive information is obtainable from Johansen's figures (1918) for the distribution according to salinity of the animals in Rander's Fjord.

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[1] In the paper quoted Prof. Cuénot regarded the differences in breeding-migration as occurring between different species. I am now informed by him that he considers the latter as varieties of *Sepia officinalis*.

No. of Marine Species.	Restricted to Salinity of
16	20-24 p.m.
9	15-24
4	12-24
0	8-24
3	6-24 p.m.
3	5-24
1	1-24

From this table (with which the figures for fresh-water forms is in substantial agreement) it will be seen that wide tolerance is rare.

If the facts assembled in the previous page seem to justify the belief that in many cases species occupy areas or habitats of different ecological character, it must not be forgotten that this may relate either to the whole life of the organism or to some critical epoch therein. Species of wide range which overlap others or are actually conterminous with them may for some crisis in the life history be far more strictly limited. The breeding period or place is a good example of this. From Shelford's description of the habitats of *Cincidela tranquebarica* and *C. scutellaris* (1912, p. 182), it seems that these beetles must overlap in distribution in the country round Lake Michigan. Their habitats are, however, very clearly defined by their place of oviposition, the former laying its eggs in moist situations, the latter in dry places (Shelford, 1908, p. 166). Such differences are probably more frequent among mobile animals ; for example, allied species of Birds may be found in the same habitats, but their nesting places may be different. The migratory tracks of the Fox Sparrows, carefully studied by Swarth (1920), bring many of the sub-species into contact ; but the ultimate destinations of the migration paths are separate. In the Pribyloff Islands the Fur Seal and Hair Seals (*Otaria ursina* and *stelleri*) sometimes herd together ; but their breeding grounds are slightly apart (Murie, 1896, pp. 222-3). Ward (1903) observed that, when several species of Bats inhabit the same cavern, the different species sleep at different levels. This observation illustrates an interesting and perhaps not uncommon mode of segregation.

Any inquiry into the distribution of allied species in relation to their environment must deal with the plastic structural response of the organism to external forces. For example, if we find two forms, which are structurally different, living in different habitats we may be tempted to argue that they may represent different environmental forms of the same species.

The salient facts concerning the plasticity of plant and animal form were outlined in Chapter II., and the hereditary transmission of the effects of the environment will be considered in Chapter VI. It is sufficient here to point out that within certain limits modification by the environment does produce what we may call habitudinal convergence, *i.e.* or the occurrence of similar forms in habitats of similar ecological nature that may be widely separated. For a remarkable example of this reference should be made to the description of the fauna of the Matlah River (India) by Kemp (1917), the numerous records of similar modifications produced in brackish-water mollusca assembled by Pelseneer (1920), and the occurrence of similar forms of *Artemia salina* in similar types of brackish pool first described by Schmankewitsch and discussed by Bateson (1895, p. 96 and foll.). Similar cases are of course even more familiar in plants (cf. Kerner and Oliver, 1895, and Warming, *l.c.*, *passim*).

In spite, however, of these facts, there remains a very obvious limitation to this responsiveness. Allied species may occur in the same habitat without any demonstrable convergence. Species of animals may range over many types of environment without visible change (Duerden, 1907). The same local races are not always produced in allied species in the same locality (Gurney, 1923[1]; Harrison, 1920 B; Sumner, 1923); while the dividing line between species may not coincide with environmental " divides " (Ruthven, *l.c.*).

It remains now to mention some special phenomena of this order. The term " geographical trends " has been coined to express the correlation of structural change with

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[1] I am indebted to Mr. R. Gurney for pointing out to me that "same locality" is susceptible to different interpretations. The validity of the above proposition depends on whether identical habits or identical areas are involved.

climatic or other environmental change which is graded over a wide geographical area. Sumner (*l.c.*) has pointed out that the geographical races of the *Deer* Mice (*Peromyscus*) in W. America are not distributed at random, but in such a way that there is a correlation between pigmentation and humidity. Similar evidence is given by Swarth (1920) in his work on the races of the Fox Sparrows (*Passarella*) of the region stretching from Alaska to California, and by Vogt (1909) for Bees (colour and density of " fur "). These examples are, of course, only special and rather striking cases of the effect of the environment on structure (to be discussed anon (Chap. VII.)); but they are important to note now because they show the effect of the environment in producing regional forms. A more complex problem, to which further reference will be made in Chapter VI., is " insular melanism ". There are many records of the great frequency upon islands of melanic forms of animals. They are to be found among Birds (Beebe, 1924; Bateson, 1913, p. 143), Lizards (Boulenger, 1913), Mollusca (Pelseneer, *l.c.*, p. 561) and Moths (Harrison, 1920, p. 245). It is also possible that species inhabiting littoral stations may show the same phenomenon (Harrison, *l.c.*, and Swarth, *l.c.*). Harrison (*l.c.*, *passim*) attributes the melanism in the case of the Lepidoptera to the fact that the latter feed on plants drenched in spray, as a result of which they take in a large quantity of salts. The experimental administration of salts (manganese sulphate and lead nitrate) is known by the work of Harrison and Garrett (1926) to produce hereditary melanism in the Lepidoptera. It does not necessarily follow that the melanism of Birds and Lizards has this origin. The matter requires further consideration, however, as far as the incidence of melanism in islands and littoral stations is concerned. The instances of this phenomenon that are on record are not numerous enough to carry conviction that it is of universal occurrence. Moreover, when we consider the amount of spray that is carried inland in littoral regions, *e.g.* in the British Isles (cf. Richards and Robson, 1927), it is surprising that parts of these islands are not encircled by a coastal belt of, *e.g.*, melanic Lepidoptera, as it should be, if the hypothesis under question has any foundation.

From the data given on pp. 99-105 it will be apparent that there are many factors which may determine the habitat of a species ; but it is likely that the whole complex of such factors determines an area of optimum conditions in which individuals of the species are most numerous, while the limits of dispersal are fixed by some critical factor. That single factors may have a decisive effect cannot be much in doubt. But it may very well be true that the limits to dispersal may not be the same in all parts of the periphery of an area. The distribution of the Mussel, *Mytilus edulis*, in the region of St. Andrews, New Brunswick, has been studied by Mossop (1921). She finds that below low-water datum the mussels are limited by the attack of enemies—starfish, sea-urchins and whelks. The upward limit is apparently fixed by the effects of exposure on the young mussel larvæ ; though it is uncertain which of the possible factors involved in exposure (light, heat, lack of food, etc.) is decisive. " The upper limit of the mussel beds is not so sharply fixed as the lower, since the protection against exposure is not equal in all locations " (Mossop, *l.c.*, p. 33).

While we must thus conclude that a general case is made out for the ecological determination of the areas and habitats of species, such determination is by no means universal. Species may occupy a very confined habitat, or they may be cosmopolitan. Still more significant is the evidence afforded by the rapid spread (often effected in a very short time) of animals and plants into new environments sometimes without any noticeable change of structure Among plants Warming cites the cases of *Senecio vernalis*, *Picea excelsa* and *Erigeron Canadensis* (*l.c.*, 364). Zoology provides us with *Paludestrina jenkinsi* (Robson, 1923), *Crepidula fornicata* (Robson, 1915), the Brown Hare (Barrett Hamilton, *l.c.*) and *Cordylophora lacustris* (Harmer, 1901). The frequent records of animals transported by human agency such as the Rabbit, the Brown Rat and the land-snails *Achatina fulica* and *Eulota similaris* may also be cited. If we find then that, given a suitable opportunity, a species may rapidly spread far beyond its original area or habitat, we are entitled to suspect that the difference of habitat as actually recorded may not be entirely a matter of adaptation. I do not wish to suggest that the dispersal of a species that is rapidly enlarging its area (*e.g.*) will not be ultimately limited by one factor or another ; but we should not be prone to assume that the actually recorded differences of habitat between allied species represent differences of adaptation. We have therefore to inquire what alternative or supplementary explanations there may be of differences of distributional area or habitat. There are two such alternatives before us. In the first place, differences of habitat may depend on a principle which we may call Opportunity Dispersal. A new species as it arises may be compelled by competition to occupy a less favoured or an unoccupied " niche " in nature for the simple reason that other habitats are already occupied. In the second place, when two species occupy overlapping areas of different size, or when the one area includes the other, or if they occupy different areas of diverse size, the differences may be due to the fact that the species occupying the smaller area may be of more recent origin than the other, and, assuming a relation between age and dispersal, have not yet spread as far as the other. The latter is the hypothesis of " Age and Area " put forward by Willis (1922). It will be seen that the two suggestions are similar in so far as neither of them explains difference of area by difference of adaptation, although in special cases differences in adaptive capacity may be involved. Moreover, the first hypothesis depends like the second on differences in age between allied species as the fundamental cause of the difference in distribution. They differ, however, in that the first accounts for the actual difference in the area occupied by two species by assuming that a " young " species is limited in its choice of habitat by the pre-existing occupants of the area in which it arises, while the second, without seriously considering the opportunities for dispersal, merely holds that a " young " species would not have travelled so far and so widely as an " old " one.

important principle by which differences in dispersal can be explained, seems to me unwarrantable. We have considered evidence which must convince us that the toleration of external factors is not the same among allied species. There is likewise convincing evidence that species have extended or contracted their range under the influence of secular changes of climate. There can be no questioning the accuracy of Willis' data, or the statistical and graphical methods by which he displays them. The only thing that seems open to doubt is his assumption that time is the only factor that can produce these results (cf. Regan, 1924). It seems that exactly the same results would emerge if wide toleration were very uncommon and limited toleration frequent (see p. 107). Moreover, the hypothesis seems to lack the essential proof which only paleontology can supply, that, *e.g.*, the widely ranging forms are the oldest.

Having thus considered the possible causes of differential distribution, it remains to say a word as to the relation between range and variability.

The relation between the range of a species and its variability can be considered in two ways. We may inquire whether there is any fixed relation of such a sort that, *e.g.*, a widely distributed species is more variable than one with a more limited distribution, and we may consider to what extent the range-variability of a species is affected by the proximity of allied species. The latter problem is dealt with in connection with Intermediacy (Chapter II., p. 28).

Darwin (1859, p. 67) gave it as his opinion that "it is those (species) which range widely . . . which oftenest produce well-marked varieties or . . . incipient species". Pelseneer (*l.c.*, p. 428) is of the same opinion. It is a little uncertain to what extent we can accept this statement as true, and the following provisos must be made. In the first case there may be considerable differences in various groups of organisms. Animals, such as sessile forms and many motile invertebrata which show marked plastic variability according to their environment, may show more varietal forms in a small area than a more active form does over a wider range. Secondly, in the same group quite nearly related forms may differ very much in their variability. Thus Coutagne (*l.c.*) records that *Helix lapicida*, which occurs all over France, is only slightly variable, while *Bulimus detritus*, which has not such an extensive range, is far more variable. According to Duerden (*l.c.*) the tortoises, *Testudo pardalis* and *angulata*, have a wide range through a diversity of environmental conditions in South Africa, but are very little variable. Chapman and Griscom (1924, p. 282) comment on the slight racial variability of *Troglodytes musculus* over a range extending from S. Mexico to Cape Horn. The snail, *Cochlicella barbara*, which occurs in many places on the West European littoral and penetrates inland in many places in France, is incredibly polymorphic in the colour-pattern of its shell. On the other hand, the shell of *Helicodonta obvoluta*, which has a more extensive range (though in different areas), is far more restricted in its variability. Many species which have a restricted range and live in uniform conditions may be very variable, as are many of the Hawaiian *Achatinellidae* (Gulick, Pilsby and Cooke, *l.c.*), while many species of wider range may in any restricted area show a high degree of polymorphism. A remarkable instance of this is seen in the land-snail, *Xesta citrina*. A series of this species from a few islands in the Soela Archipelago, obtained in 1920 by the British Museum, show a positively bewildering range of colour and pattern. Very probably one would conclude that degree of variability is a matter of individual idiosyncrasy, though such species as inhabit a large number of different habitats and are at all restricted in their individual range are likely to be more affected by external conditions. It is also pertinent to inquire what the standard of variability is. In the paper on the House Wrens above quoted, Chapman and Griscom comment on the " surprisingly little racial variation " over a wide area. The differentiating characters are very slight, but some eighteen forms are described. It would be very difficult to decide the value of an instance of this sort *vis-à-vis* a species having a more restricted range in which the varieties were less numerous, but more distinct. Sometimes the proposition will be compromised by the taxonomist's varying standard of a species, the reduction of many species to varietal status having the automatic result of enlarging the varietal content of species.

CHAPTER V

ISOLATION AS A FACTOR IN THE DIVERGENCE OF SPECIES

ALTHOUGH Darwin was willing to concede that Isolation (*i.e.* geographical isolation) must have played an important part in the production of new species, he was not prepared to assign to it a conspicuous part in the evolutionary process. The importance of isolation was recognised by Lamarck (see Packard, in Gulick, 1905), and Darwin's contemporary, M. Wagner, elevated geographical separation to a position of paramount importance. Subsequently Romanes (1886) drew attention to the rôle of sexual isolation (" physiological selection "), in which he was followed by Petersen; while K. Jordan further developed the idea of geographical isolation. In a work which deserves considerable attention, Gulick (1905) analysed the effect of the various modes of isolation, and in addition stressed the importance of difference in seasonal appearance, habit and " occupation ". More recent authors have dwelt upon the importance of the second of these (Plate (1913); Cuénot (1921); Regan (1925)).

By " isolation ", as the term is used in current biological literature, we usually mean spatial separation. By implication, however, we are actually concerned with any mode of separation that prevents the production of fertile offspring from the union of two distinct species. We thus come to speak, *e.g.*, of two species being isolated by incompatibility[1] or by mutual sterility. In short, the most important aspect

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[1] " Incompatibility ", as used in this work, implies psychological aversion from pairing with another individual.

of isolation is its effect in debarring species from fertile unions.

Species have been described as isolated by divers means—by topographical barriers, by the occupation of different habitats within the same area, by difference in habit and "occupation", or by some impediment to successful reproduction. The latter may consist in (1) difference in the structure of the reproductive organs ("mechanical isolation"); (2) the choice of partners of one sort and the avoidance of others ("selective mating", "psychological isolation"); (3) difference in the breeding season ("cyclical and seasonal isolation", Gulick); and (4) sterility. Difference in mating habits is to be regarded as involved in (2).

Before we attempt to study the way in which the various factors likely to produce isolation are operative in nature and the extent to which their incidence is correlated with structural and other divergence, we should ascertain what theoretical grounds there are for thinking that isolation is of importance in promoting divergence.

The prevention of intercourse between two sections of a population is not, of course, assumed to give rise *per se* to new forms. If, for example, a certain area becomes isolated from the neighbouring parts and its animal population is found to exhibit characters not found in the population of the adjacent territory, those characteristics can only have arisen through the agency of one of the principles currently held to bring about the origin of new forms, viz. "Mutation", induction by the environment or Natural Selection. How far one or all of these principles may be important in causing divergence will be considered anon (Chapters VI.).

Isolation is held to be of importance in preventing forms which have become divergent from being resumed into the general population. We believe that each divergent strain is kept from intercourse with other strains by some bar to successful intercourse, and the object of this chapter is to ascertain how far this is found to take place.

To many writers on evolution some measure of isolation is regarded as a necessity in order to account for the persistence of a new character which would, if conferring no substantial advantage on its possessor and exposed to the dangers of "swamping" (*i.e.* obliteration by continuous cross-breeding), rarely survive. This difficulty, as far as it referred to single characters, seemed removed by the discovery of unit-character inheritance. The difficulty, however, remains in spite of this discovery. If a new character arises as a simple segregate, either dominant or recessive, it will not, of course, be obliterated by "swamping".[1] There is no necessity to invoke isolation in order to explain how such characters persist. If, however, the new character is the product of a change in many factors, or if more than one character-change is involved, then the matter is not so simple. In many species-crosses, especially among animals, mid-intermediacy, either of single or many characters, and divers varying combinations of the parental characters are of very frequent occurrence. From such mid-intermediates or recombinations, the parental characters or combinations would only be recovered very occasionally, if unrestricted and continuous interbreeding took place.

New characters having a complex factorial base and new combinations of characters will only be able to maintain themselves if they are subject to some measure of isolation. The only other way in which a system of several characters could be maintained would be some hereditary mechanism which would secure the permanent association of such characters, and the segregation *en bloc* of the factors responsible for them. There is, as we shall see, some evidence for the occurrence of this mechanism, and it will be discussed in Chapter VII.

Gulick (*l.c.*, p. 152) considered that one of the ways in which isolation promotes divergence is by separating portions of a population which do not represent the average character of that population. Cuénot (1921, p. 402) makes the same

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[1] We perhaps ought to distinguish between actual modification of a character through the contact of its factorial base with other factors and the failure of individuals having a given character to hold their own or increase numerically. By "swamping" we mean the former of these alternatives.

claim, " parce que les groupes séparés pouvaient à l'origine ne pas renfermer les mêmes génotypes, étant donné que c'est aux confins de sa distribution géographique que l'espèce présente les formes les plus éloignées du type moyen ". I do not understand why Professor Cuénot particularly instances the part of a population at the confines of its distributional area as more subject to isolation than any other part. It is certainly true of, *e.g.*, the fauna of the edge of a continent, from which islands might be separated. But there are many other modes of isolation which might isolate more central portions of a population, and the latter are liable to contain individuals which deviate from the mean of the whole population. In any case such an effect can only be a work of supererogation ; for if a section separated from the main mass of a population differs from the latter at the time of isolation, we have still to seek for the origin of that divergence, though we shall grant that isolation may preserve such preliminary divergences.

This suggestion, however, is of considerable importance. There is no doubt that populations made up of the individuals of a species frequently contain genotypically diverse element, the origin of which does not immediately concern us. If such a population is distributed over its area without restriction to intercourse, except in so far as individuals very remote from each other are not likely to pair, there will be a general diffusion of the characters over the whole population, the only tendency to isolation arising from the distance which separates individuals from one another. Not a great deal is known at present concerning the differences and relationship between the various parts of a natural population. ✓In molluscs like *Helix aspersa* or *Cepea nemoralis* in the British Isles the same variants tend to occur in areas as remote from each other as Cornwall and parts of Scotland. If, however, a population is broken up by topographical barriers or other hindrances to intercourse, parts of such populations may possibly be isolated before they become morphologically differentiated.

Attention has already been drawn (Richards and Robson,

1926) to the fact that in a population of animals with "colonial" habits, colonies which are fairly remote from one another will tend by the accumulation of differences of habit, breeding season, etc., to attain to complete isolation, though each colony will not perhaps differ from its immediate neighbours sufficiently for this to occur. The distribution of individuals of a single species in "colonies" is a phenomenon requiring much attention, and I am not altogether certain that the term "colony" is correctly applied in all cases. If by a "colony" we mean a self-contained, permanent association arising from a gregarious tendency, it is correctly applied in some cases, *e.g.* in certain genera of Insects (e.g. *Zygaena*) and Birds. In a species split up into such colonies there will always be a strong tendency for parts of the original hereditary stock to be sharply segregated. If, however, the "colonies" are merely accidental "patchiness" due to the inroads of enemies or fortuitous disposal, such chance associations will sooner or later be merged into the general population. Captain F. M. Davis of H.M. Fisheries Laboratory, Lowestoft, has conducted for several years a massive investigation of the distribution of *Spisula subtruncata*, a small clam which is preyed on by fishes on the Dogger Bank. Though it is not at present certain that some ecological factor (soil) is not involved, it seems to me quite likely that the remarkable "patchiness" recorded by Davis (1923) may be due to the inroads by fishes into the bottom-fauna, or, as Davis evidently thinks possible (*l.c.*, p. 20), to the drifting of larvæ in various directions by varying currents, such larvæ travelling some distance before they settle down on the bottom. (See footnote, p. 103.)

In the light of what was said concerning the heterogeneity of natural populations, it must be evident that isolation may be absolute or partial. Two strains may be rigidly debarred from producing fertile offspring, or the barrier to intercourse may be less rigid. Certain individuals of a species may be fertile with those of another species ; but other examples of the two species may be mutually sterile. Some members of one species may be in contact with another species, and others may be isolated from the latter. In short, theoretically speaking, the homogeneity of a species or a race is proportionate to the strictness of its isolaton.

Part of the ground of this discussion has been already traversed in the preceding chapter, in which we saw that many species occupy habitats or areas distinct from their allies. It will be necessary, however, to return to this subject, in order to discover how strict such topographical isolation may be, and to what extent it is reinforced by asyngamy.

Having thus seen the general grounds on which isolation is deemed to be actually effective, we must now consider the various modes of isolation and their inter-relationship.

A. Sexual Isolation

Two species are debarred from producing fertile offspring by any of the following means :

(1) differences in (*a*) breeding season, and (*b*) breeding place ;

(2) psychological repugnance from or failure to be stimulated by
  (*a*) recognition marks (Rassengefühl (Plate)),
  (*b*) scents,
  (*c*) courtship antics,
  (*d*) mechanical stimuli ;

(3) mechanical disharmony of the copulatory apparatus ; and

(4) various disharmonies in fertilisation and development (reviewed in Chapter III.).

Some or all of these have been described by various authors ; but the data presented in the following discussions are perhaps somewhat fuller and more integrated.

It should be understood that, while any one of the disharmonies mentioned above may establish sexual isolation, the others are by no means necessarily involved at the same time. Thus Harrison (1916*a*) has already shown in his crosses of Lepidoptera how in different pairs of species sexual isolation is established by different sexual disharmonies. Staples Brown (1923) found that certain species of Pigeons may copulate without repugnance, but with negative results ; while conversely Harrison (*l.c.*, p. 98) gives a case in which fertility is accompanied by repugnance.

(1) (*a*) *Breeding Season.*—As an index to the extent to which differences in the breeding season may limit interbreeding between allied species, we may take from Lo Bianco's records (1909) of the period of sexual maturity of marine animals living in the Gulf of Naples, the figures for Mollusca and Crustacea.

	Mollusca.	Crustacea.
Number of pairs of species of the same genus	37	52
Breeding seasons coincide in . . .	6	7
,, ,, differ in . . .	7	12
,, ,, overlap in . . .	23	33
,, ,, doubtful in . . .	1	0

From Bent's account of the habits and distribution of North American wild fowl (1925), I have collated distribution and period of reproduction (from the egg-records). By far the greater number, nearly all in fact, of the contrasted species belonging to the same genera, both when the range overlaps and when it is distinct, have breeding periods which widely overlap.

The breeding periods of different races or varieties of the same species are known to differ sometimes. This is recorded by Heincke (in Regan, 1925) for the Herring of the Baltic and North Sea, by Smith (in Plate (1913)) for *Crangon* and *Orchestia* in the Mediterranean, by Cuénot for *Rana esculenta* and *Rana esculenta ridibunda* (1921, p. 414), and for *Sepia* (1917). When the amount of overlap in the breeding season is only moderate, the chances that two allied species of overlapping distribution will have an opportunity to interbreed must still depend on the occupation of like habitat. So that before any of the further bars to fertility (psychological, etc.) are considered, we must envisage a considerable amount of isolation arising from the conjunction of different habits and somewhat different breeding periods.

It is needless to say that our knowledge of the breeding period is very incomplete, and in very few groups is it well enough known to enable us to say how frequently it gives rise to isolation.

(*b*) Differences in the breeding place have been already discussed (Chapter IV., pp. 105 and 107).

(2) *Psychological Barriers* (" Isolement psychique ", Cuénot, "Rassengefühl " (Plate)).

Among species which inhabit the same area and habitat, and at the same time have identical or overlapping breeding periods, a bar to successful union may arise through either indifference between the males and females of different species or active repugnance on the part of one to the other. The males of a species may be habitually endogamous, or the females of one species may actively resist the advances of males of another species.

However, although the members of a certain species might habitually select partners from among themselves even when representatives of another species were present, they might not show repugnance to the latter, if they alone were available.

It is uncertain whether unwillingness to pair with another species is a widely spread phenomenon. The records of hybridisation in captivity and numerous field-observations make it fairly evident that coitus with another species is by no means uncommon. At least one case is known to me (Harrison, 1916, p. 98) in which the male of a species, when caged up with females of its own and of another species, preferred to pair with the latter. Pairing inclination is, however, not necessarily an index of morphological affinity, as Harrison (*l.c.*) and others find that representatives of distinct genera pair readily, while species of the same genus (e.g. *Philosamia cynthia* and *promethea*) may show disinclination. Nor is disinclination to pair necessarily an index of actual sterility, as the eggs of one of the species last named can be artificially fertilised with the sperm of the other (Harrison, *l.c.*, p 98).

Preferential mating is recorded in several groups, and many examples are given by Darwin (*Descent of Man*, chap. xiv.) and others. In Birds it is often noticed in consequence of the formation of colonies occupying distinct but adjacent " territories " the members of which do not interbreed. Thus the Common Guillemot (*Uria troile*) and the Ringed Guillemot (*U. ringvia*), which occupy different ledges on the same cliffs, have never been seen to mate. Again, we must note that such segregation does not necessarily imply the sterility of the species in question, as Cuénot (1921, p. 413) states that the Common and Hooded Crows, which live thus segregated, are mutually fertile.

" Selective mating " has been reported in lowly organisms, *e.g.* in *Paramoecium* (Plate, 1913), while in the Algae Crow (1924) records observations of Archer, who noted that in *Micrasterias* " like forms or species conjugate with like forms or species, even when individuals of the same species are rare and mixed with more abundant individuals of other species ". Crozier (1918) and others have shown that selective mating can take place within a species. Large and small individuals of the Nudibranch *Chromodoris* studied by Crozier tend to pair with those of their own size. Actual size, however, does not always constitute a bar to coitus, as I have taken a specimen of the snail, *Cochlicella barbara*, 16 mm. in length, with the penis inserted into an animal little more than half its size. Harrison (1916, p. 100) notes that *Lycia hirtaria* and *Poecilopsis pomonaria* contrive a successful union in spite of disparity in size, and Racovitza (1894) observed the union of a male *Octopus vulgaris* with a female less than half its size.

Repugnance to coitus has been noted between many allied species, and even between races and varieties of the same species. It is recorded in Mammals (*e.g.* Detlefsen, *Cavia* (1914)), in Birds (Staples Brown, *Columba* (*l.c.*)), Pulmonate Gastropoda (Diver, *Cepea* (MS.)), and in Insects

(Morrison, 1924). The records of Ackerman (*l.c.*) should be consulted. I am inclined, however, to think that this is not a very widely spread phenomenon, for the instances of complaisance are very numerous, as the literature of genetic experiments testify. Repugnance is probably most marked in animals which have highly differentiated mating-habits, and I suspect that it attains its maximum in Mammals and Birds.

The actual basis of repugnance is not easy to ascertain, and it may depend on a generalised objection to the total sum of perceptible differences or on a special reaction against a particular attribute or act. It may be necessary to distinguish also between violent antipathy and a mere failure to respond to a particular stimulus. The former may lead to violent and hostile repulsion, if coitus is attempted ; or it is possible that coitus may be tolerated without producing the necessary physiological reaction which in some cases must be the prelude to fertilisation. It is impossible, however, to press this inquiry further, as I am not familiar with exact data on which to found such distinctions. It is sufficient to note the occurrence of violent antipathy (*e.g.* in *Cavia* (Detlefsen, *l.c.*) and, in animals less closely related, the Hare and Rabbit (Castle, 1925)).

The extent to which any particular feature of behaviour or means of excitation is definitely repugnant to members of a different species is difficult to ascertain. The rôle of scent glands, special markings, mating antics and mechanical stimuli as a means of isolation is possibly important in certain groups. For example, Petersen (1904, p. 423) lays great stress on the scent glands of Lepidoptera as a bar to coitus. My friend Captain C. Diver informs me that the snail, *Cepea hortensis*, seems to " resent " the dart of *C. nemoralis*. That olfactory stimuli are important in mating is shown by Sturtevant's observations (1921, p. 10) on *Drosophila*. Males and females of *D. melanogaster* were placed in vials in which other pairs had just copulated, and as a result they paired significantly sooner than males and females placed in clean vials.

It is, however, obvious that it would be often impossible to distinguish the actual basis of repugnance, to decide (*e.g.*) whether it was due to the recognition of distasteful or unfamiliar colour, scent or behaviour.

With regard to the divers means by which the sexes advertise their presence to each other from a distance (*e.g.* song, vibration of feathers, drumming with the beak or wings in birds, stridulation in insects), it is a little uncertain to what extent the recognition of a note or other sign made by another species is a deterrent. That some of these mating-calls or signs are markedly specific is undoubted. One of the most remarkable instances of this is to be seen in McDermott's discovery (1917) of specific differences in the flash emitted by Fireflies (*Lampyridae*). It is likewise certain that males and females of the same species respond to each other's peculiar call or sign. I can find, however, little evidence as to how the call or sign of a different species is received.

(3) *Mechanical disability.*—Inability to copulate owing to differences in the structure and size of the external genitalia has been observed in various groups of animals and commented upon for many years. Recently the subject has been carefully examined by Boulangé (1924) in respect to the Hymenoptera and allied groups. I am not aware that a similar exhaustive study has been made of the copulatory apparatus in other groups in which that apparatus is extensively differentiated (*e.g.* Pulmonate Gastropoda, Trematoda and Mammalia).

Before we consider the special group studied by Boulangé and the opinions of this author, we should very briefly survey the differentiation of the reproductive apparatus in the animal kingdom.

✓ In sedentary animals and those which liberate their reproductive cells into a fluid medium, such as the Coelentera, Sponges, Polychaeta, Echinoderms and some Mollusca, the secondary reproductive organs are scarcely differentiated at all. In groups in which fertilisation is internal, or in which the eggs are fertilised when still adhering to the body of the female (as in many Crustacea), intromittent organs and organs employed for clasping the female are developed and may become very complex, while additional complexity is found in the development of accessory organs for the storage of spermatozoa (spermathecae). It seems, however, that the complexity of the reproductive apparatus is not an immediate sequel to the attainment of a mode of fertilisation involving coitus. Many Prosobranch molluscs in which fertilisation is internal have a very simple copulatory system little subject to specific differentiation (*e.g.* Buccinidae), while in others it is very complex (*e.g.* the Neritacea).

In studying the complication of the copulatory system for our present purposes, we must consider in what way a mechanical bar to coitus may ensue therefrom. In a group like the Crustacea the oviduct and vas deferens are very little complicated. If any difficulty is encountered in coitus between species, it must be in the adjustment of the abdomens of the male and female, in posture and in the structure of the male clasping-organs. In forms in which fertilisation is internal, additional difficulty must be encountered in the shape of the penis and vagina and in any special armature of the former as may occur (as in some Mammals and Ophidia), and in the size and form of special devices for conveying spermatozoa (spermatophores of some Pulmonata, Cephalopoda, Crustacea, spiders, etc.). In all cases we must envisage a very considerable specialisation of the musculature subserving coitus.

To what extent these various differences in the mechanism of copulation are subject to specific differentiation of an order likely to introduce isolation is extremely uncertain. The most clear case seems to be when the copulatory organs of both sexes are rigid and of a special shape as in many insects, or when the penis has an internal support (*Baculum* of Mammalia) of varying shape, or is provided with hooks (Nematoda, Mammalia). It is a little doubtful to what extent differences in posture, clasping-organs, musculature, etc., may lead to isolation by themselves, though very probably in conjunction they may serve to do so.

The complicated shape of the chitinous intromittent and receptor organs of Insects has received a good deal of attention in the past, and has given rise to the "lock and key" theory of isolation. According to the latter the male organ fits into the female as a key into a lock, and only a key cut with appropriate wards can actuate each lock. Such a precise adjustment of the copulatory organs of the two sexes would, if found to be of general occurrence, be a very important means of isolation. The subject has been reviewed by Boulangé (*l.c.*), who supplies a valuable historical sketch of this and other theories of isolation. The gist of Boulangé's review and criticism, which relate to the Hymenoptera, is as follows:

A. The evidence of Strohl and others makes it quite evident that differentiation of the copulatory apparatus in these insects is not always specific.

B. The differentiation of these organs, when it occurs, is almost always characteristic of the male and not of the female apparatus. The key, to maintain the simile, may have characteristic wards, but the lock is of a universal pattern.

C. If isolation occurs as a result of differentiation of the copulatory organs, it must depend on "l'adaptation de l'ensemble de l'appareil à la production des mouvements nécessaires à l'accouplement". Boulangé points out that instances are known (e.g. *Osmia rufa*) in which the individual variation of copulatory organs is often not correlated with other structural divergences, for the individual variability within a species may exceed that between other distinct species.

We should recall the number of successful pairings that have been obtained in other Insecta (e.g. *Lepidoptera*), in some of which the copulatory organs are different in the species crossed. Thus the moths, *Nyssia zonaria* and *Lycia hirtaria*, can be successfully crossed, although the male genitalia of the two species are different (Harrison, 1916, p. 134 *f*, plate v., figs. 1 and 5). In some of these pairings, in which the copulatory apparatus permits of natural fertilisation, the unions may be nevertheless sterile.

In short, then, although we know that the copulatory organs are specifically different in many Arthropod groups (Coleoptera, Lepidoptera, Hemiptera, Diplopoda, Isopoda, Arachnida (Cuénot, 1921, p. 416), we are very far from knowing to what extent they constitute a bar to coitus. In all probability they are not, even in those groups in which they are most markedly differentiated, a source of complete isolation in themselves, but may be so in conjunction with differences in posture and musculature. I do not think there is any need at the present time to consider seriously the question as to whether the acute differentiation of the copulatory apparatus and its adjuncts seen in some groups is adaptative. The view that they are produced to prevent crossing and "to maintain the purity of the race" does not require serious consideration. The marked specific diversity of the generative organs in some groups is a very striking fact. It is all the more remarkable when we consider that in some groups of similar evolutionary status they are little diversified. But at present there is no satisfactory explanation of this difference.

(4) The various disharmonies in fertilisation and development which constitute sterility in the strict sense of the word have been considered in Chapter III.

B. Topographical and Habitudinal Isolation

From the facts given in the preceding chapter, it will be apparent that allied species are found either in the same areas or habitats or in different ones, and it would be very difficult to say which is the more frequent type of occurrence. We found some grounds for thinking that much depends on the type of organism, that species of Birds, Mammals and Reptiles, for example, tend to occupy different areas or habitats, while invertebrates seem to be less restricted. Whatever may be the cause of this, it is plain that topographical isolation is by no means universal.

At the same time we saw that species which have identical areas of distribution may be nevertheless isolated because they occupy different habitats within such areas. The extent to which areas of distribution or habitats are rigidly demarcated from adjacent areas or habitats so as to give rise to complete isolation, is very difficult to state in general terms, and it is very likely that many species which actually occupy different areas are in contact with their neighbours at the periphery of their territory. Topographical and habitudinal isolation is more advantageously discussed in relation to sexual isolation (p. 133); but some special points may be noticed here.

(1) When we think of definite barriers to dispersal it seems that, although they may be summarily described as topographical, they are almost invariably rooted in habitudinal differences. A desert or a range of mountains are obstacles to certain types of mammal (for example), because they involve the intervention of different life-zones. I stress this rather obvious fact because in the case of some obstacles it seems that we must distinguish between the obstacle itself and the life-zones into which it may be ecologically divisible. Thus a species habituated to life at high altitudes may cross the summit of a mountain range, but on each side it may not be found below a certain height.

(2) The species or races which live in lakes or river-systems, in islands or in any circumscribed situation, may appear to be rigorously isolated; but much depends upon whether such forms have habits or modes of reproduction which tend to maintain the isolation or to promote the wider dispersal of the species. Small invertebrates, such as some molluscs or crustacea, may be transferred from one situation to another by divers means (cf. Kew, 1895, and p. 144), so that isolation in as secluded an area as a mountain tarn may be more apparent than real, and the degree of isolation will be proportionate to the frequency of some adventitious mode of dispersal (*e.g.* by Birds). A few chance transferences of individuals of a lacustrine species of mollusc from one lake to another by Birds or some such accidental transport are not likely to affect the character of the population into which such forms are introduced, though they may be effective if

there is little competition within the latter, and if the food supply is ample.

(3) In all probability prolonged topographical isolation is followed by complete sterility. It may often be very difficult to prove that the sterility was the outcome of such separation and was acquired slowly. But such a series of observations as those of Harrison (1916) on the Bistonine moths lead one to assume that the longer the period of (in this case) geographical isolation the more complete does sterility become. Instances are, however, on record of fertility between forms geographically or habitudinally separated. Thus the Saturniid moths, *Actias lunae*, an American form, and *A. selene*, which occurs in India, are fertile (Przibram, 1910, p. 48). Harrison (1913, p. 130) has shown that *Lycia hirtaria*, which usually feeds and oviposits on birch, is tolerably fertile with *Poecilopsis pomonaria*, which preferably feeds on oak and hawthorn.

(4) I ought perhaps to point out that isolation does not necessarily involve differences of environment. Two sections of a population occupying a uniform territory may become isolated by differences in the reproductive organs or by the development of selective mating. It is even possible that forms which are topographically isolated may occupy habitats that are virtually identical. Many of the species of *Achatinella* studied by Gulick in Hawaii (*l.c.*, p. 20) and of *Partula* observed by Crampton in the Society Islands (1916 and 1925) are topographically isolated, but the areas occupied cannot be held to be different in any important ecological factor.

It is of course very difficult to show that habitats in widely separated geographical areas can be identical. It is always likely that even if the physical, geological and climatic conditions are the same the associated fauna and flora will not be identical, so that competition and other vital issues will not be the same, though, as has been pointed out, the general conditions may be " sufficiently similar for the amount of divergence attributable to them to be (relatively) unimportant " (Richards and Robson, 1926). In more adjacent areas it is likely that the difference will be still less.

C. Of habits that form a basis for isolation other than those connected with mating and those that are more strictly considered as habitat-occupation, it is difficult to find many examples. Among active animals the obtaining of food can perhaps be regarded as not dealt with under the second category. But while many species (*e.g.* among insects and land-snails) undoubtedly tend to feed on different food-plants, etc., it is difficult to find records in which the total range of food-plants is known, so that it is not easy to estimate the actual amount of difference or overlap.

Conclusions as to the Interactions of Modes of Isolation

The extent to which these presumed causes of isolation are actually operative is uncertain in some cases. For example, differences in the copulatory apparatus must not be taken to prevent successful intercourse, for species with differently shaped male organs have been successfully crossed. Spatial and habitudinal isolation and differences in habit, etc., cannot be held to be absolute bars to successful intercourse among contiguous species, unless they are accompanied by actual sterility. As Gulick has pointed out (*l.c.*, p. 127), " spatial isolation prevents organisms from crossing only when isolated in space. . . . Many slightly divergent forms arising through local isolation are [? may be] reintegrated with the surrounding forms ", and it is only if during such separation isolated species acquire other divergences (of which the most fundamental is sexual isolation) that they become finally isolated. In practice one finds that the habitat, breeding season and " occupation " tend to overlap, so that none of these can be regarded as absolute modes of isolation. Two species may have different food-plants and yet be quite fertile, so that there is always a chance that individuals of the two species may meet and effect a fertile union, if the food-plants happen to be adjacent and to appear at the same time. Nevertheless, such partially effective means of isolation may result in a complete bar to intercourse, if they act in conjunction. The chances that two members of different species otherwise fertile *inter se*, which have different food-plants, different breeding seasons and habits, will be able to effect a successful pairing are very small. In stating that sterility is the fundamental basis of isolation, I do not, of course, wish to imply that divergence may not arise if two forms are isolated for a long period by topographical barriers or by some critical difference in habits. All I wish to suggest is that, if two such forms are not mutually sterile, the degree of their isolation will depend upon the efficiency of the geographical or other barriers.

Inasmuch as structural divergence is found between mutually fertile species, it will be seen that " sterility is not necessarily a primary cause of isolation " (Richards and Robson, 1926), and, as a result, of structural divergence. In many cases sterility, no doubt, will be the result of some other mode of isolation if prolonged and exclusive. Harrison (*l.c.*) has conclusively shown that it increases with progressive geographical isolation and duration of time. It is obviously impossible to make any other generalisation as to the most effective mode of isolation, except that " when interbreeding is not stopped by any of these means (differences in habits, etc.), sterility may yet make it effective " (Richards and Robson, *l.c.*). Differences in mating and other habits, " occupation " and selective mating cannot, of course, become operative among plants and sessile animals. Differences in habitat, distribution and the breeding season, sterility and selective pollination (among plants) are the only means of isolation among these organisms. Of these it is probable that the first three are rarely absolute among closely allied species. This circumstance, combined with the absence of differential mating and other habits and of selective mating, should a priori favour a higher incidence of hybridism among plants and sessile animals than among more active organisms. There are, of course, several well-known instances among plants (*e.g.* among the Roses) of multiple hybridism resulting from the absence of marked sterility, and similar instances will no doubt be recalled among sessile and highly localised invertebrate animals. But I do not think the matter has been sufficiently examined to enable us to assert positively that hybridism is commoner among these than in the more active forms.

Having thus reviewed the chief modes of isolation, and having seen to what extent some measure of isolation accompanies structural divergence, it is now desirable to take stock of the converse of this, and ascertain how far and, if possible, at what rate divergence proceeds when isolation is known to intervene. It is one thing to establish a presumptive case that divergent forms are isolated from their allies by certain means ; but we require to know a little more precisely how isolation intervenes in the production of divergent forms.

It will be best to consider the effects of topographical isolation in this context. If, as is sometimes shown, very closely allied forms, or forms barely recognisable apart, may be mutually sterile (see p. 78), we do not know how long that sterility has been established, so that we cannot properly gauge its effects. It is otherwise, however, in certain instances of topographical isolation in which we can, within certain broad limits, estimate the time of isolation.

It is of course generally recognised (cf. p. 118) that isolation by itself does not give rise to actual divergences between the various parts of a population. Its rôle is confined to preventing such divergent sections from interbreeding. It will not be amiss to review in detail an instance of racial and specific divergence, in which it is difficult to disentangle the effects of topographical isolation from more remote causes of divergence, and to assign to the former its proper importance.

The acute local polymorphism of the Achatinellid land-snails of the Sandwich Islands studied by Gulick is by now a text-book commonplace ; but it is well suited for our purpose, as it has been recently reviewed, with a wealth of ecological and other data, by Pilsbry, Hyatt and Cooke (*l.c.*).

I use the latter source of information more frequently in this summary. The islands in which this phenomenon has been studied are often cut up by radiating ridges into series of deep valleys. Contrary to the received opinion, the snails do not now inhabit the valleys as much as the ridges. Gulick speaks of them as mainly occupying the valleys ; but, from Pilsbry and Cooke's account, it seems that they have of recent years been more restricted to the ridges (1912, p. xxxvi.). On the latter persists the jungle which has escaped the deforestation which has affected the valleys, and in this mass of vegetation the snails find a degree of moisture which they cannot obtain in the valleys. It is known from the presence of shells in coastal sand-dunes (*l.c.*, p. xlix.) that sixty years ago the snails ranged much lower down than they do at the present time. Whether the development of the marked local forms now restricted to the ridges antedated the process of restriction is uncertain. However that may be, the fact remains that on the ridges are found a great number of highly localised species, each ridge sometimes possessing its own peculiar form. It should be particularly noted : (1) that the later workers, applying more critical methods, reduced Gulick's 200 species to 43, while they multiply the varietal forms ; (2) that restriction of species to single ridges is by no means the rule, for many species obviously spread over more than one valley-system (e.g. *Achatinella fulgens* and *vulpina*) ; (3) that the distribution may be even more sharply localised than that usually described, for several species are restricted to single trees or groups of trees (Pilsbry and Cooke believe the latter are either (*a*) remains of moribund species, or (*b*) new mutations) ; and (4) that there is gradual regional change (as opposed to sharply differentiated local races) in some groups, which may extend through several valley-systems.

The part which topographical isolation has played in this episode is obscure. In the first place, although much differentiation has occurred in the valleys and on the ridges, it is apparent that not all the species are so confined, that species may be even more intensely localised, and that on the other hand gradual regional change occurs in some cases ; so that isolation by valleys and ridges is not the universal rule. In the second place, although admittedly the circumstances are somewhat unique and of an order specially favourable to the isolation of sections of a population of land molluscs, in that they consist in the reduction of forest vegetation in the lower reaches of the valleys, the deforestation is comparatively recent. Sixty years ago the snails were found well below the attitude to which they are now restricted (cf. *l.c.*, p. xlix.-l.). If isolation has been influential in the origin of the specific diversity in the valleys, it has taken effect at a remarkably fast rate. Thirdly, though as we have said the conditions of isolation are especially favourable, it is a little difficult to understand why in many other places topographically as suitable as the Hawaiian valleys, such acute polymorphism has not been found. Admitting, for example, that the upper ends of the Swiss valleys are usually not cut off by life-zones inimical to land-snails, it is a little strange that in the valleys of the Valais, for example, some of which are deeply recessed, so few cases of restricted local races are reported (Piaget, 1921). The same is true of some of the deep and secluded combes of the south of England, especially in localities such as some of the coastal combes of Cornwall, between which there is no continuity of life-zones.

Gulick (1905) and Pilsbry and Cooke (*l.c.*, p. xxxii.) all agree that, as far as can be ascertained at present, the intense diversification of these forms is not correlated with any differences in the vegetation, climate or other vital conditions of the various valleys.[1] Crampton (1925) stresses the same point in the similar local polymorphism of the Partulas of the Society Islands. As the matter stands at present, we have no proof that isolation preceded differentiation ; so that it is just as likely (indeed more probable) that before the carving of the ridges became at all pronounced there was very great evolutionary activity, which gave rise to numerous

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[1] Pilsbry and Cooke make a provisional exception to this generalisation. They believe, however, that the correlation indicated (height of station and banding of shell) is of an indirect nature.

mutant races which were imprisoned in the vegetation of the different ridges as they became isolated. That the evolutionary circumstances may have been exceptional is indicated by the following facts : (1) at the present time the snails breed all the year round ; (2) according to Pilsbry and Cooke the present population, judged indeed by purely phenotypic characters, shows traces of frequent hybridisation ; (3) the animals seem to be living in optimum conditions.

It seems to me to be uncertain how far the acute local " speciation " seen among these snails has been influenced by their actual restriction to the ridges and valleys. From some of the facts one is inclined to believe that the isolation now seen has been brought about in comparatively recent times, and has contributed very little to the racial and specific divergences which may have been due to more remote and less perfect causes of isolation which originally segregated the population into colonies. I feel that, though no more is claimed for isolation than its ability to maintain and promote already existing differences, it is desirable to make this criticism, because in the past undue emphasis has been laid on the part played by topographical segregation, as illustrated by this instance.

Some of the best known cases of divergence through topographical isolation are to be found in the faunas of oceanic islands, of which it is unnecessary to supply illustrations. If one inquires whether there are any examples of oceanic insular species which have *not* diverged, great difficulties are encountered ; for it is not easy to make sure that such forms as have not diverged are not recently introduced by accidental transport. Only a very strong case founded on some critical factors in the habits of an animal can disprove introduction, or the very fortunate accident of its discovery as a fossil in strata old enough to qualify it for long residence on the island. An interesting case of this sort is provided in the mollusca of the Bermudas, for an introduction to which I am indebted to my friend Lieut.-Col. A. J. Peile.

Gulick (A.) (1904) lists a certain number of molluscan species which are found in Bermuda and the adjacent islands and mainland. These forms were critically considered by Pilsbry (1900), who decided on good evidence that a certain number were introduced by Man. The rest he assumed to have come in by oceanic transport. Now of these forms (eight in number), two at least are known as fossils in Æolian limestone ; so that we find that three species have been resident on the island for a long time and are unmodified. I do not cite this case as definite evidence that a species may live in isolation for a long time without modification. The age and origin of the Bermudan fauna may be still contentious matter. It warns us, however, that Darwin's doubts (*Origin of Species*, p. 128) as to the effects of insular isolation may be valid, though we may not be inclined to agree with the grounds on which he based his doubt.

When we turn to consider non-oceanic islands and their fauna, we find that the divergence of the latter seems to proceed in a very capricious fashion. On the Ilhéo de Cima, a small islet some 1200 metres in length, which lies off the larger island of Porto Santo in the Canary group, is to be found a remarkable and very distinctive endemic species of snail, *Ochthephila turricula.* The channel between Cima and Porto Santo is only 300 metres in width, and is very shallow (3-4 fathoms). Now we may ask why this species of snail has become differentiated on Cima, while in the Inner and Outer Hebrides, many of which are separated by greater distances and deeper channels from their mainland, not a single endemic species of snail has been reported, nor indeed any well-marked variety.[1] According to Cockerell (1922, p. 270), the environmental conditions of Cima and Porto Santo are the same. Now we have seen that isolation itself probably has nothing to do with the actual production

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[1] It cannot be said that the malacological survey of the Inner and Outer Hebrides is complete A good many of the islands have been investigated from this point of view, and the only instances of divergence I can trace are certain slight statistical differences in the shells of *Limnea pereger* and *Paludestrina ulvae* recorded by Annandale (1922).

of new forms. According to the current view, this depends on the environmental conditions (acting either directly or indirectly through selection) in which isolated forms develop, or on chance mutants. Isolation merely maintains the new form. If this is the case, it need not surprise us that a new mutational form should occur on Cima. But how is it that not a single endemic species or variety is known from the Hebrides, with its numerous islands? If variation preceded purely at random and at an equal rate, then it is not unreasonable to expect that we should find some endemic forms in the Hebrides. There are three possible explanations of this apparent anomaly: (1) the channel between Cima and Porto Santo may be older than those between, *e.g.*, Harris and the Scottish mainland, its depth having no relation to its age; (2) since their isolation, the Hebridean snails have been in a quiescent state as far as variation is concerned; or (3) human communication between the Hebrides and the mainland may have continually introduced enough mainland snails to prevent the formation of local races.

The lack of differentiation in the Hebridean snails stands out in sharp contrast to what is known about another group of animals in this area. Thanks to the work of Messrs. Barrett Hamilton, Hinton, Ogilvie Grant and Montagu, we are in possession of a great deal of information concerning the mammals of the Inner and Outer Hebrides, some results of which we may now describe.

My friend and colleague, Mr. M. Hinton, tells me that at present we are far from certainty as to the range and amount of variability of the various insular species and varieties that have been described from this area, and we have already seen that in one case the taxonomic status originally assigned to an insular form has been modified as a result of further investigation. There is every reason, however, to believe that, even if further modifications of this sort are made, they will not seriously minimise the amount of local divergence among those animals. On the other hand, it is by no means certain that absence of recorded diversification in a given group of islands necessarily implies that such local diversification does not exist. All that absence of such records may imply is that the islands in question have not been fully explored. The following account is given subject to this qualification, and rather as an interim report on the present state of our knowledge on an interesting case of insular speciation than as a final verdict as to the rate and manner of divergence under isolation.

Apodemus sylvaticus sylvaticus, the Common Bank Mouse, occurs widely on the mainland and the islands, including the Shetlands ; yet on Bute it has given rise to *A. sylvaticus butei.* Now the island of Bute lies very near the mainland, and some of the islands on which the parent form occurs are far more remote, *e.g.* the Shetlands. It is conceivable that Bute may have been isolated longer than the Shetlands ; though we do not know whether it was separated from the mainland in pre- or post-glacial times. We cannot, however, believe it has been longer isolated than Skye, which is known to be pre-glacial in origin, and yet no local form of *Apodemus sylvaticus* is yet recorded from Skye. Must we explain this by suggesting a more frequent contamination of the Skye population from the mainland (which is most unlikely), or by appealing to "special conditions" on Bute ? Again, *Microtus agrestis exsul* occurs on Arran, Jura, Mull, N. and S. Uist and other islands, while on Muck a special variety *M. agrestis luchii* is found, and another variety, *mial*, occurs on Eigg. Great Cumbrae has its own form of *Apodemus hebridensis*, but its shrew (*Sorex araneus*) is the mainland form. Shetland and Fair Isle have the same variety of *Apodemus fridariensis*, while the neighbouring island of Foula has its own variety (*thuleo*). In what way are we to interpret this apparently irregular and haphazard differentiation, if indeed we are entitled to consider that the data are actually reliable ? Is it mainly dependent on the time of isolation, so that the longer a form is isolated the greater chance it will have of diverging ? is it dependent on a quite irregular and capricious rate of variation, on the initial variability of these small rodents that was characteristic of the population before sundry elements became isolated? or on special external conditions which evoke change in one island and not in another? Lastly, we must inquire if human interference and accidental transport in special cases may not hopelessly confuse the issue, and prevent us from deciding between an indigenous form and one quite recently introduced.

In the first place it seems very unlikely that, *e.g.*, the divergence of *Microtus agrestis luchii* on Muck is due to "special conditions" realised on that island and nowhere else. Nothing short of an intensive ecological survey can of course provide a final answer to this suggestion. But it seems very improbable that Arran, Jura, Mull and N. and S. Uist are so identical ecologically and Muck so unique, that only on the latter was *M. agrestis exsul* subjected to adaptive modification or direct transformation by the environment. The same scepticism must be extended to the origin of *Apodemus fridariensis thuleo* on Foula and other similar cases. Let us next consider the time-factor. The action of this may seem established, *e.g.*, in the case of the Jura and Islay shrews, of which that inhabiting the more recently separate Jura is more like the mainland than the Islay form (Montagu, 1922, p. 931). The only means at our disposal for judging the time of isolation are the distance from the nearest mainland and the depth of the channels. The latter is not a very satisfactory criterion, it must be admitted, when the various factors which may hasten or retard the formation of a channel are considered.

From information very kindly supplied to me by Dr. J. Horne, F.R.S., it is apparent that the dates of the submergences that cut off the various islands cannot be determined with sufficient accuracy for our purposes. In a general way we can say that N. and S. Uist, Benbecula, Skye, Mull and others of the Western Isles, are of post-Eocene and pre-glacial origin, and that the Shetlands, Fair Isle and Foula are probably post-glacial. But it is impossible to decide the relative dates, *e.g.*, of the isolation of Foula and Fair Isle, and of Mull and Muck.

If, however, the criteria of distance from the mainland

and depth of channel are accepted we might admit that Foula, which is separated from Mainland (Shetland) by a channel averaging 40 fathoms and a distance of about 16 miles, is likely to be more recently separated from Mainland than Fair Isle, which is distant from the latter 24 miles, over an average depth of about 70 fathoms. Nevertheless, the Bank Mouse of Fair Isle is the same variety that is found on Shetland, while Foula has its peculiar variety. Again, the Outer Hebrides are separated from Skye, which on account of its immediate proximity to the coast of Ross we will regard as mainland, by some 14 miles of sea (from Ard Renish on Harris to the west coast of Skye) and a channel of a much greater average depth than that between Eigg and the Ardnamurchan mainland, which are about 7 miles apart. Yet *Microtus agrestis* has the same variety (*exsul*) on Skye, N. and S. Uist and Benbecula, while Muck has its own local variety, *luchii*.

We might finally invoke the habits of these animals and their possible transference by human agency from time to time to those islands in which no noticeable divergence has taken place. One of the particular genera which we have been considering, viz. *Apodemus*, may well be subject to such accidental transport, for the animals sometimes frequent human habitations. My colleague, Mr. Hinton, tells me that *Microtus* is not likely to be carried from island to island by Man.

It thus appears that we are not really in a position to decide what the circumstances favouring divergence are in this instance. Within the limits of our knowledge we find that divergence has proceeded apace in some islands, while in others there has been no differentiation. On a given island one form may diverge and another may not. In the present imperfect state of our knowledge the evolution of these forms seems to be purely capricious and to be dependent on the particular state of variability of the animals in question rather than on time of isolation or the external circumstances of their environment.

Some interesting results have been obtained as the result of plankton surveys of some of the lakes of W. Europe, particularly with regard to the Crustacea. Burckhardt (1900), as a result of a survey of the larger Swiss lakes, came to the conclusion that a distinction must be drawn, as far as local diversification is concerned, between forms which have " resting eggs " (Dauereier) or a " resting " phase and the ordinary acyclic forms. He produces evidence that the former do not tend to give rise to local races, while acyclic forms like *Daphnia hyalinia* and *Bosmina coregoni* manifest "colonial" variation. This phenomenon is very clearly manifested by the *Bosmina*, as its colonial forms are found along with less differentiated types. If this view is strengthened by a large series of observations, it will lead irresistibly to the conclusion that success in the production of local races in lakes, etc., depends in this group of animals on the absence of a means whereby a fresh supply of individuals can be introduced from the outside. The " resting " eggs are that means, for they can be transported by accidental agencies such as birds, and perhaps gales of wind. (Mr. R. Gurney, in considering the crustacean plankton of the English lakes, expresses doubt, however, as to the efficacy of transport by birds (1923, p. 426).)

Confirmation of this view seems to be derived from the study of the crustacean plankton of the English lakes made by Gurney (*l.c.*). In this series there is very little local differentiation, except in the cases of *Daphnia*, *Bosmina obtusirostris* (cf. Burckhardt) and *Cyclops abyssorum*. However, if we admit that a particular factor in the life history, such as the presence of " resting " eggs, may successfully break down isolation, and, confining our attention to forms in which the isolation is complete, attempt to gauge the effects of isolation in particular cases, we do not find it acting with any degree of uniformity. Thus Gurney (*l.c.*, p. 445) finds that *Bosmina obtusirostris* in Crummock and Buttermere, two of the "primitive" English lakes, is different from the form in the more " evolved " type of lake. But in Ennerdale, which is likewise a primitive lake, the *Bosmina* is not so divergent as that of Crummock and Buttermere, its size being close to that of the form found in Ullswater and Derwentwater, the antennal length being like that of forms found in the latter lake, and the length of the mucro approaching that found in specimens from Floutern Tarn. In contrast to what is found in the Swiss lakes, when *Bosmina coregoni* (which is very closely related to *obtusirostris*) shows very great local variation, Gurney states that in the majority of the English lakes " the differences shown by the Bosminas are not, I think, outside the limits of their ordinary variation within a single population ".

The lacustrine forms of Molluscs in W. Europe, and in particular of the British Isles, are not at all well known as yet from the point of view of the statistical study of racial differentiation. A few examples are worth considering however. Mr. A. E. Stelfox, who has made an exhaustive study of the small Pea Clams, *Pisidium*, of fresh-water, has informed me that a number of the latter obtained by Mr. O. W. Richards and myself in out-of-the-way streams and ponds in the Scilly Isles are either " environmental forms ", forms found elsewhere, or are otherwise normal. Surbeck (1899) finds that in the Lake of Lucerne, " eine lokale Fauna hat sich nicht ausgebildet ", and, as far as the available records are reliable, the same seems to be true of such of the English lakes as have been studied.

A species such as *Limnea pereger* may give rise to innumerable local forms. But in using the shell as diagnostic of species great care must be exercised. In the British Isles, *Limnaea involuta* and *L. praetenuis* were regarded as strictly localised lacustrine species. Quite recently, however, both forms have been recorded from other lakes (Stelfox, 1911, p. 110), and from Mr. Stelfox's account of *L. pereger* (*l.c.*, pp. 109-10) it seems that, in isolated tarns of the West Coast of Ireland, local forms of that species are to be found which approach *involuta* and *praetenuis* in the shape and texture of the shell. According to Mr. Stelfox, *L. pereger* is very much subject to local differentiation, " each tarn having a distinct form of its own " (*l.c.*). It is still uncertain what the status of these local forms may be. The shell of this species is known to be very readily modified by experiment, and until we know something of the genetic behaviour of such forms we cannot regard them as true local races of fixed heredity.

It is no exaggeration to say that we are only just beginning the study of the intimate causes of local differentiation, and much time and study is necessary before we can produce an explanation of these phenomena in any particular case.

I have insisted in the previous pages upon the apparently capricious divergence of forms isolated in comparatively recent times.[1] It may very well happen that in the future these forms will be more intensively studied, their bionomics fully elucidated, and the causes of their divergence or non-divergence fully explained. That this should be done is highly desirable, for it is to those first beginnings of divergence that we find in racial differentiation that we turn with the greatest interest. As the matter now stands, it seems that neither peculiar local conditions of environment nor any regular rate of variation proportionate to the time of isolation can be systematically invoked as causes of divergence, but that the variation is sporadic, highly irregular, and quite often independent of external factors.

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[1] It is very necessary to emphasise the fact that more intensive collecting may explain many apparent anomalies (cf. p. 140).

PART II

CHAPTER VI

THE ORIGIN AND SPREAD OF VARIANT CHARACTERS

IN this chapter and the last we shall discuss the origin of variation, the numerical increase of the individuals bearing new hereditary characters, and the nature and intensity of the correlation that is established between all the characters which differentiate allied species one from another. It is not my aim to discuss those larger problems of evolutionary theory which deal with the history of organs and the broad tendencies that have been noted in the progressive development or decline of groups of animals and plants, though in the last chapter I shall try to indicate the relation between these wider issues and our more restricted inquiry.

Some doubt has been expressed as to the right of positive science, in this case of Biology, to pronounce a final verdict on the manifestations of life. According to Bergson (1911, p. 206), positive science, being a work of pure intellect, when it undertakes the study of life " necessarily treats the living with the inert ", and " the truth we thus arrive at . . . is no more than a symbolic verity ". He considers (p. 208) " that the inert enters naturally into the frames of the intellect, but that the living is adapted to those frames only artificially, so that we must adopt a special attitude towards it, and examine it with other eyes than those of positive science ".

I am prepared to believe that M. Bergson is correct in this view; but at the same time I think there is still a legitimate sphere of study open to the biologist in evolutionary inquiry, to which he may confine his attention without any danger of trespassing into other fields. He may collect and co-ordinate the data of evolution in virtue of his special knowledge, and he must decide whether his particular hypotheses as to the transformation of animal and plant life are in themselves valid. I agree with M. Bergson that science, theory of knowledge and metaphysics should meet on the same ground. But I feel that not only must they " pool " their effects, but that each must test its affirmations by its own appropriate technique. For this reason I have not in the discussion that follows taken the subject out of the strictly biological field.

In enumerating the various theories by which the process of evolution has been explained, one experiences some doubt as to the propriety of treating certain of these as separate and self-contained conceptions. The doctrine of the inheritance of induced variation and that of Natural Selection are self-contained theories standing in a reasonable amount of antithesis to each other. The body of data and opinion that has gathered around the nucleus provided by Mendel's discovery and the work of de Vries has no such clear-cut individuality. We may indicate it by such names as " the doctrine of Mutation " or " Genetics ". But although they may be justified as indicating a different approach to evolutionary phenomena, these names are frequently used to suggest a conception of the process of evolution distinct from those already mentioned. Actually we have moved away from the earlier position of an acute antagonism between Natural Selection and the findings of genetical research. The term " mutation " has come to acquire a significantly different meaning from that which it formerly had, and in the eyes of many students the antithesis between Natural Selection and the findings of genetic studies is no longer of real significance. This question will be more fully dealt with on p. 175. In the meantime I think we may say that this antithesis is far less profound than that between the two doctrines in question, and the belief that all new hereditary characters are impressed on the organism by its environment. Nevertheless, as has been repeatedly pointed out, Darwin himself believed that hereditary variation was partly referable to environmental causes, and this view is taken by some modern geneticists.

A few students have adopted a standpoint not considered in the orthodox biological theories, which attributes the transformation of plants and animals to an internal impulsion. The Orthogenesis of Eimer is in practice a special form of modern " Lamarckism " ; but the " Momentum " of Dendy, the " Programme Evolution " of Kitchin and Lang, and the " hormic " impulse of Russel all assume an internal directive force which is traced, at least by Dendy (1912) and Lang (1921, p. 24), to a physiological origin. I have not attempted to discuss these principles at any length. My object has been to ascertain how far the more orthodox theories are capable of explaining unaided the initial stages of evolutionary divergence. If there is a place in our biological philosophy for one or another of the principles that involve the recognition of an impulsion that, either from within the organism or from without, guides it along paths not laid down by adaptation and chance, it should be apparent as a result of this discussion; but it is not my intention to take it for granted that such appeal to an impulsion is required until the more orthodox views have been carefully examined.

I have said above that there are three principal theories which have been claimed to give an explanation of the process of evolution on orthodox biological grounds. The value of each of these may be judged by its ability to give an acceptable account of the origin and multiplication of the small hereditary differences between closely allied species. To do this they must account in the first instance for the origin of any single heritable difference. They must next explain its spread in the population in which it arises. Finally, they must account for the origin of groups, such as taxonomic species, in which several such characters are differentiated and manifest that amount of correlation which enables us to recognise individual groups.

The use to which the three chief hypotheses have been put in explaining the various processes involved in evolutionary divergence is not the same. Environmental change is held by some to be capable of causing hereditary modification. But those who hold such views rarely consider how far the groups of individuals which receive their peculiar attributes from such a source have been conterminous in their distribution with the special environmental factors which are assumed to cause such peculiarities Nor do they explain how organisms are dispersed beyond the area in which such factors are operative, and why, if the main hypothesis is correct, we do not find a large measure of local convergence among all the allied forms which inhabit a single area (see p. 174). The doctrine of Natural Selection, while it provides an explanation for the numerical increase of a given type, supplies no exact account of the origin of variation and largely assumes that the latter is spontaneous. The same is true of the doctrine of Mutation ; and, in addition, those exponents of the latter who do not accept the doctrine of Natural Selection have never been seriously concerned to show how individuals carrying " indifferent " (*i.e.* non-advantageous) characters can increase numerically.

The Origin of Variation

It is now universally recognised that many forms found living in nature and described as varieties and species are the products of local environmental conditions. Purely phenotypic variability (*Accommodation* : Cuénot), so widely recognised in plants, is familiar in animals as well, and is seen either as slight fluctuations in size, density and colour, or as more definite changes of form and arrangement of parts. The general responsiveness of plants and animals to environmental stimulus was described in Chapter II.

Experiment has shown that many of these modifications persist only as long as the environmental conditions remain unaltered, and we need not doubt that a great deal of the variability and intervarietal and interspecific difference found in nature is of this order. Structural modifications known through experiment, or the facts of correlation to be produced by the environment, do not merely consist of alterations of substance and dimension. We should note the following instances of special modification :

Organism.	Modification Produced.	Author.	Modification caused by
1. *Daphnia* .	Hooded carapace	Woltereck	Temperature.
2. *Artemia* .	Increase in number of separate segments	Schmankewitsch	Salinity.
3. *Leptinotarsa* .	Pattern	Tower	Temperature.
4. *Simocephalus* .	Flanging of carapace	Agar	Food.
5. *Scrophularia* .	Alteration of leaf margin	McDougall	Chemical reagents.

The specific action of chemical substances upon particular structures is further seen in the selective elimination of the kinetonucleus of Trypanosomes by Oxazin (Laveran and Roudsky (in Dobell, 1912)). We may note also that a single factor, viz. increase of temperature (cf. 1 and 3 above) can produce dissimilar effects, and (2) that the same modification can be produced by dissimilar causes, *e.g.* darkening of pigmentation in *Arctia* by heat (Fischer), in *Vanessa* by carbonic acid gas (V. Linden, 1904), and in *Scardafella* by humidity (Beebe, 1907, cf. also Swarth, *l.c.*).

The susceptibility of plant and animal structure to environmental stimuli, whether it be as passively received modifications or as response to stimulus in the narrow sense, fulfils one of the preliminary conditions of "Lamarckism" in its old and new guise. To what extent such modifications of the parental soma or alterations directly induced in the germ cells are hereditary is at present uncertain. On the other hand, I do not think the evidence that hereditary variation is purely germinal is any stronger or more convincing. Indeed, it is at the present time quite impossible for a candid investigator to form a positive opinion as to whether hereditary variation is germinal or *ectogenic*. Some authors have felt constrained to assume an agnostic attitude (cf. Newman, 1921, p. 364), while others (*e.g.* Babcock and Clausen, 1918) believe that hereditary variation may be due both to internal and external causes. This is the opinion I have adopted in this work, but I know of no evidence that assists us to decide which of the two causes is the more important.

It is generally thought that heritable variation must either result from an automatic change in the nuclear material of the germ cells, or be imposed on the living organism by external forces.[1] No information is available as to the nature of the actual automatic changes in the nuclear material which are presumed by some to give rise to new structural characters ; so that a final and conclusive account of purely germinal change is wanting. If we may judge by analogy with chemical and physical phenomena, it seems very unlikely that the long history of purely germinal change which is thus presumed, resting as it does on chemical and physical activities, could have proceeded indefinitely without any external stimulus at all. The suggestion has been made that the genes presumed to be responsible for the production of visible characters are of the same nature as catalysts, and as such are liable to modification by external influences. A discussion of this view, with references to the relevant literature, is to be found in a paper by Schmalfuss and Werner (1926). An analogy has been suggested (Huxley, 1926) between automatic germinal change and the spontaneous internal transformation of radio-active substances. Mr. J. B. S. Haldane has likewise pointed out to me that the radioactivity of Potassium (present in all cells) is quite enough to account for occasional disturbance of the germinal material.

A. The Evidence that Inherited Variation is Germinal in Origin

The facts which compel us to believe that automatic germinal variation may take place independently of the environment are as follows:

(1) When animals have been kept under standard cultural

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[1] The likelihood that heritable variation may also arise from the interreaction of germinal and external change is also entertained. See pp. 170-72.

conditions, variation has occurred which cannot be attached to any environmental cause (*Drosophila*, *Gammarus*). It has been argued that the circumstances of captivity and abnormal diet have influenced the production of the *Drosophila* mutants. As these animals are normally scavengers (Sturtevant, 1921, p. 15), and the diet given in cultures is actually the sort of pabulum to which they are accustomed, this criticism cannot have much weight.[1] Moreover, the isolated and sporadic appearance of the mutants does not suggest an environmental effect which should affect if not all the experimental animals, at least a larger part thereof.[2]

(2) Any one who has combined a study of variation with field work and ecological observation will be struck with the fact that the same type of variant is not always produced in allied species in one and the same locality (Harrison, 1920 B, p. 63, and cf. chap. iv., p. 108). Berg's study (1926) of this subject leads one to infer that, when local convergence occurs, it is of a special nature. A certain amount of local parallelism occurs if the conditions are in any sense abnormal (*e.g.* in estuaries, torrents, sand dunes), and as we have satisfied ourselves that a great number of species are to be regarded as occupying different or overlapping habitats, even if they superficially appear to be identical in distribution, we should not expect to find a very large amount of local convergence. Moreover, we have reason (p. 153) to believe that diverse structural effects may be produced by the same causes. Nevertheless, if the environment were the sole cause of variation we would expect to find more similarity in the variant characters of local populations than we actually encounter, especially among those species which have more or less identical habits, food, etc. This lack of local convergence may be explained away by various arguments, *e.g.*

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[1] A special environmental influence may be suspected in the production of the same type of mutant (eye-colour) in *Drosophila* and *Gammarus* where the two forms are kept in cultures. Although the coincidence may seem significant, we must, however, remember that at least in *Drosophila* eye-colour resembling that of the mutants observed in cultures is found in nature (Sturtevant, 1921, p. 120).

[2] For a fuller discussion of this point, see pp. 170, 235-6.

that all the forms in a given habitat are not in an appropriate physiological state to receive modification, or that some of the species in such associations are new-comers and have not yet been transformed. A similar difficulty in the way of a belief in the transforming power of the environment is to be met when species are known to have changed their habitat and distribution without a corresponding change of form (Chap. IV., p. 110),[1] and also when others have manifested change of form in conditions in which there is the strongest suspicion that no environmental difference is involved (cf. Chap. V., p. 137). Counter-arguments of a nature analogous to those just put forward may be introduced to explain away these difficulties. Thus Crampton's statement that the diversity of the *Partulas* in the Society Islands (*l.c.*) is unaccompanied by any corresponding environmental differences, may be challenged on the ground that the environmental conditions are not exhaustively known. But the *onus probandi* rests with those who seek to supply an environmental cause in such instances as those just cited.

(3) In nature we continually encounter allied species living side by side in the same environment, and, conversely, many species are known to range over a variety of habitats without any correlative change of structure. It is claimed, however, (*a*) that allied species living in the same environment may nevertheless at some critical phase live apart or subsist on different food ; and (*b*) that a widely ranging species may keep to the same type of habitat. It will be clear, I think, from what was said in Chapter IV. that we are very ignorant of the nature of the environmental complex in which most species live, and of the differences and similarities between their environments. Certainly nothing could be less helpful than unverified assertions that the environments of allied

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[1] One of the most striking examples of the latter phenomenon is that described by Bartsch and Quick (1926). *Zonitoides arboreus*, which normally lives under the bark of decaying trees, is sometimes found in earthworm burrows at and about the roots of sugar-cane in Louisiana. Bartsch and Quick, after an intensive study of series from both habitats, could find no difference in shell-character, digestive system (including the radula), reproductive organs or central nervous system.

species are like or unlike. In no case with which I am familiar can we say with certainty that the life-histories of any two related species are passed in identical conditions. But in many instances they seem to be so alike that any differences that do occur must be relatively trivial, and we would require very convincing proof that they are capable of producing the structural differences that distinguish the species. It is sometimes argued that differences of structure found in species occupying the same habitat were acquired elsewhere, and that the species came to live together subsequently to the origin of these differences. This is of course likely, though proof should be forthcoming that it is true in any particular case. But it involves the admission that in any case a large number of species do live together without visible convergence, and that for that reason the local environment is very frequently without effect.

(4) As will be seen later (p. 170), even in those instances which seem to provide clear evidence that induced modifications may become hereditary, it is possible that the external stimuli are selective, and act upon individuals whose germinal constitution is different from the bulk of the population.

(5) If we come to the conclusion that the direct modification of the germinal material by the chemical and physical factors of the environment is the only type of heritable change that can be produced on animals and plants by external causes, the facts of sexual dimorphism must be regarded as inexplicable on any other grounds than purely germinal variation. In this type of polymorphism we can, I think, rule out unconditionally any differences of habitat as the source of structural divergence. On the other hand, differences in secondary sexual characters have been explained by Cunningham (1920) as the results of the use of special parts by the male during courtship. The validity of this hypothesis in its various aspects is discussed under separate headings on pp. 163 and 217.

In this discussion of the origin of germinal variation I have included no description of the recent work upon differences in the number of chromosomes and the phenomenon of polyploidy. The latter subject has been recently reviewed with a wealth of detail by Professor R. R. Gates (1924). I feel that the relation between apogamy, polyploidy and hybridisation is more adequately dealt with by a specialist; but at the same time I would venture the opinion that it has not yet been made clear to what extent the phenomena of chromosomal reduplication are of importance in evolution. That there is some fixed relation between morphological change and an increased number of chromosomes is, I think, clear from the work on *Oenothera* (Gates, 1921, p. 10). But it is not to my mind clear how reduplication of chromosomes affects the characters produced by factors, or combinations of factors, which are actually carried by the chromosomes.

B. The Evidence that Induced Variation is Hereditary

This subject has been so often discussed and the evidence so exhaustively criticised that I shall refrain from presenting more than a brief sketch of the salient facts. The reader is referred to detailed discussions by Bateson (1913), Newman (1921), Macbride (1924), Kammerer (1924), and to an excellent summary of work and observations up to 1925 published by Detlefsen (1925).

If heritable variation is caused by the response of the organism to external stimuli, it may arise in two chief ways:

(1) through a modification impressed on the parental soma being transmitted to the germ-cells contained within the latter, or

(2) through a direct modification of the germinal material.

The latter may be brought about by a change affecting: (*a*) all the germ-cells of the individuals involved, or (*b*) only those which by reason of their special physiological condition or genotypic constitution, respond to the stimulus.

By " induced variation " we mean variation which is brought about either by some factor or factors in the environment of an organism, or by such factors operating in conjunction with some activity on the part of the organism itself.

The term includes in its connotation: (1) lesions; (2) passively received modifications of a non-lesional nature (*e.g.* alterations in colour and substance produced by a quantitative or qualitative change of the chemical or physical factors of food or medium); (3) formative responses to stimuli (*e.g.* alteration of mode of growth due to current- or wave-action, " effects of use "); and (4) the effects of disuse.

From a consideration of some of the more important data, I have been led to believe that it is to the chemical and physical factors of the environment acting directly on the germ-cells that we are best entitled to look for external causes of heritable variation.

There are two circumstances which must incline us favourably to the conception under review. On the one hand (cf. p. 153), the almost universal occurrence among animals and plants of somatic plasticity fulfils a preliminary condition of this theory. On the other, we must recognise the likelihood that, if the activities and substance of the germinal material are subject to ordinary chemical and physical laws, variation in that material may be due to external physical and chemical stimuli rather than to automatic change. The difficulty of explaining how somatic modifications may be transferred to the germ-cells still remains, and an appeal to hormones and the results of experimental embryology (MacBride, 1914, pp. 652-4; Cunningham, 1921) does not readily obviate it. It is likely that, if an animal undergoes a change of habit and structure its physiological processes will undergo a corresponding change, and it may be ultimately shown that special secretions, which have been thus altered or engendered, reach and modify the reproductive cells. But of this course of events and the appropriate physiological mechanism we require more satisfactory proof than is available at present.[1]

Our evidence for the inheritance of modifications either of the germ cells or of the parental soma is of two kinds—observational and experimental.

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[1] For experiments which are held to prove the transference of somatic modifications to the germ-cells, see Appendix, p. 256.

I. Observational Evidence

(a) *Correlation of environmental differences with differences of structure presumed to be hereditary*

The attention of field naturalists and systematists has of recent years been drawn to the occurrence of what are called environmental or geographical "trends" (*v.* Chapter IV.). Thus a series of allied forms which replace each other successively, *e.g.* from north to south, or from an area of great humidity through regions of increasing dryness to one of marked aridity, is noted as exhibiting some progressive modification, which is correlated with the geographical and environmental change.

So far, the bulk of our knowledge of such forms is purely taxonomic, but there is proof that some regional phases are hereditarily stable. Sumner (1923) has studied such a " trend " intensively in connection with his work on the races of the Deer Mice (*Peromyscus*) of California. He shows, for example, that there is a correlation between pigmentation and humidity. But he was unable to establish a direct causal relation between the two. Mice of different colour-types transplanted to La Jolla showed no change of colour, though bred through two to ten generations in the new environment. We might reasonably require a longer series of experiments before concluding that no change could be wrought by such transplantation. The experiments may be, however, assumed to prove that the colour in question was of a fixed heredity. But they do not prove that the peculiarity is due to a particular environmental stimulus. Sumner proceeds to show that other characters of the species of *Peromyscus* exhibit " trends ", *e.g.* a structure such as the foot becomes larger the further north the animals are found, but there is no obvious correlation with special climatic or other conditions.

One of the most instructive cases from this point of view is that of the well-known lacustrine Crustacean, *Limnocalanus macrurus*, which has arisen independently in many places as a variant from the brackish-water *L. grimaldii* of the Baltic and Caspian Seas and the coastal waters of Siberia and Alaska. The divergence of these forms has been studied by Ekman (1914) and Gurney (1923). The evolution of *L. macrurus* is instructive from many points of view, of which we can only mention here the fact that its divergence from *L. grimaldii* seems to be dependent to a large degree on the progressive freshening of the lake-systems which it has inhabited since the close of the Glacial Period. However, although, as Gurney (*l.c.*, p. 428) points out, the effect of change of medium has generally been in the same direction, the various lacustrine forms are not always alike. For example, the newly discovered form in Ennerdale Water (Cumberland) is unlike the Baltic forms. The modification of the various American and European forms, though probably in the beginning they were all similar deviations from *L. grimaldii* due to the acquisition of a fresh-water habitat, has evidently taken on different aspects in various areas. It is quite uncertain why the Ennerdale form diverges so much from the Baltic area type, while the North American forms differ from the latter so little. Gurney (*l.c.*, p. 430) regards them as " of more recent origin " (in view of the nearer resemblance to *L. grimaldii*). This may be true ; but it is merely an inference from structure.

A large body of observations has been accumulated concerning the distribution of colour-forms of Lepidoptera and the correlation of pigmentation with temperature gradients. Many colour-forms are undoubtedly the result of " accommodation " and are not of fixed heredity. On the other hand, experiments on *Abraxas grossulariata* (Schröder), *Arctia* (Fischer), and *Vanessa* (Standfuss) are claimed as proving that induced modifications of colour analogous to those manifested by the geographical races are inherited. These results are subjected to a searching criticism by Bateson (1913, pp. 191-4), who admits that the facts are undeniable, but expresses the opinion that (*a*) Schröder's *Abraxas* is "easily influenced by cultural conditions" and that the original parents were "abnormal", and (*b*) that the forms studied by Standfuss and Fischer are subject to great variation (*i.e.* (?) germinal variation which cannot be distinguished from induced change). I cannot help thinking that these criticisms do not wholly destroy the value of the evidence, though it must be admitted that such experiments should be conducted upon stock of which the genotypic constitution is exhaustively known.

Jordan (1892),[1] Berg (1926), and others have noted that in the fresh-water and marine fishes of Europe there is a general reduction of the number of vertebræ in the series of forms encountered as one proceeds from north to south. The same is noted by Hubbs (1925) for marine fish of the Pacific. This reduction is somewhat vaguely attributed by Berg (*l.c.*) to the effect of the " geographical landscape ", *i.e.* to the sum of the environmental factors characteristic of a given region.[2] He does not actually claim that such a modification is strictly speaking hereditary, but one infers that this is meant. I do not know that we have any proof that the various stages in the reduction of the vertebræ are not acquired anew by each generation. In a similar way the decrease in size that has been noted in the shells of Molluscs inhabiting southern waters, as compared with their larger northern representatives (Pelseneer, 1920, p. 516; Hesse, 1924, p. 165), may be purely a somatic modification.

More facts of a similar nature could be cited as well as cases of " epharmonic convergence " (Vesque), *i.e.* the acquisition by different species of a similar facies when living in identical conditions (Berg, 1926), and the correlation of structural differences with peculiarities of habitat (cf. Annandale (1924)); but in only one case, that of the acquisition of melanism by Lepidoptera in industrial areas (Harrison and Garrett, 1925, to be discussed later), have we evidence (*a*) that a special environmental factor can be shown to evoke the definite structural peculiarity, and (*b*) that the change thus evoked has become continuously inherited. As we have reason to believe that the " industrial " melanism described by Harrison and Garrett is good evidence for the inheritance of an environmental modification, we are bound to consider

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[1] Jordan (*Proc. U.S. Nat. Mus.* 14, p. 107). Not in Bibliography.

[2] Reduction of vertebrae correlated with decreased salinity by Heincke (summary by Williamson) (*Fisheries, Scotland, Sci. Inv.*, 1914, i.).

seriously some of the other instances of the correlation of melanism with special habitats (*e.g.* among Birds and Lizards, cf. Chapter IV.) ; but we await the proof that such melanism is of the same origin as that in Lepidoptera.

The separate items of evidence presented in this section are not then, save in the case of the melanic Lepidoptera, of such a nature as to convince us that modification induced by a change in the environment is hereditary, though collectively they are perhaps significant.

(b) *Observations on the Effects of Use and Disuse*

So much evidence is available from human heredity that speaks against the inheritance of the effects of use that it may seem superfluous to discuss the matter. Nevertheless there are some special instances which require examination.

Among mammals and birds that adopt the kneeling posture callosities are formed on the skin at the points where the weight of the body is supported on the ground. It has been stated (see Duerden, 1920) that these callosities appear in the embryo. If this is true, it might seem to constitute a proof of the inheritance of the effects of use. But it is not possible to decide from these facts, whether the callosities were acquired through selection of germinal variation, or whether continued use was influential on the germinal material. The only way in which we could set about proving this would be to induce an animal to acquire an entirely new habit, as a result of which some somatic modification would be acquired, and ascertain if the latter became inherited. (See Appendix.)

A similar series of observations is assembled by Pelseneer (*l.c.*, p. 687), from which we may take a single example. Pelseneer following Jackson (" Phylogeny of the Pelecypoda") states that the byssal sinus of the lower valve of the scallop (*Pecten*) is a variation acquired as a result of the pressure of the byssus, consequent on the assumption of the horizontal position. The sinus is hereditary, and in the development of the individual it appears before the animal fixes down by the byssus, and is thus not produced anew in ontogeny at least by the assumed mechanical stimulus. We cannot accept this statement as a proof that a structure acquired through pressure becomes hereditary. We do not know that the sinus is actually produced by the pressure of the byssus in the special circumstances of the change of posture. We cannot help feeling that it might have been thus produced; but clearly we required some proof of this (see anon under 4, Embryological Evidence).

The progressive atrophy of disused organs or parts has been often explained by assuming that the effects of disuse are inherited in a cumulative fashion. In discussing this subject we have to confine our attention to such instances as involve the association of atrophy with some definite cause of disuse, *e.g.* the association of blindness and depigmentation with the cavernicolous habit. Nevertheless, there are other types of atrophy and degeneration less definitely attributable to a known cause, *e.g.* the degeneration or loss of the shell in many Gastropoda and Cephalopoda; and we have to admit that many animals show degenerative tendencies not easily to be referred to external or functional causes.

Though there are many instances of various kinds in which atrophy seems to be associated with disuse, it is best to confine our attention to the phenomena most satisfactorily explored and reinforced by experimental evidence, viz. the instances of loss or degeneration of eyes in cave-dwelling animals.

Although there are many records of blindness in cave-dwelling animals, the cavernicolous habit does not always lead to this condition. Cuénot (1925, p. 207) cites instances of normal vision in Fish, Amphibia and Mammals. Kemp (1925, p. 20) records only four instances of blindness among 102 species inhabiting the Siju Caves in Assam. It may easily be argued that such animals are new-comers; but such a contention is in need of proof. Payne (1910) subjected *Drosophila ampelophila* to continued darkness for sixty-nine generations without obtaining any modification of the eyes, though in the end the reaction to light was slightly impaired.

But there is a further difficulty involved. We do not know with any certainty whether the atrophy is caused by the lack of light, or whether animals sightless from other causes survive in caverns because they are not exposed to the attacks of enemies. The only way in which we could resolve this dilemma would be by ascertaining if deprivation of light regularly induced the atrophy of the eyes. Beyond Kammerer's experiments on *Proteus*, which he claimed to prove that the degenerate eyes of a cave-dwelling form could be restored to a normal condition by exposure to light, I know no positive evidence that shows that the development of the eye is absolutely determined by the amount of light.[1] Another difficulty that confronts us is that we cannot as yet distinguish with certainty whether the structures which we have been discussing undergo *progressive* reduction (*a*) because the structural and physiological degeneration induced by lack of the stimulus is cumulative in the course of inheritance, or (*b*) because the amount of stimulus (*i.e.* light) is gradually reduced, because each generation penetrates further into the cave which it inhabits. The occurrence of normal and reduced eyes has been recently studied in the deep-sea Octopoda (Robson, 1926). When allowance is made for our ignorance of the habits of these animals, and when we invoke sources of illumination other than sunlight to account for the occurrence of species with normal eyes in the oceanic depths, we still find ourselves in grave difficulties when we attempt to relate the size of the eyes of these organisms to other indications of abyssal habitat revealed in their structure. Thus we find in certain species that, while the eyes are not reduced, the ink-sac is degenerate or absent, a feature suggestive of lightless conditions.

I do not think that we should dismiss the alleged inheritance of the effects of disuse as undeserving of serious consideration ; but it is plainly in need of verification and cannot be regarded as evidential. On the other hand, the contention that, *e.g.*, animals with atrophied eyes are found in caverns and other lightless places because they can survive there and nowhere else, is just as much in need of verification.

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[1] See, however, Kapterew in Kammerer (1924, p. 175).

(c) *Characters which are not Heritable in some Species and Heritable in others*

It has been pointed out that in certain allied species identical morphological characters may be heritable in one case and non-heritable in another (Richards and Robson, 1925, p. 383). The exploration of this type of evidence is very much to be desired. Its importance resides in the fact that some of the non-heritable characters which have hereditary analogues in other forms are either known to be of environmental origin or to be correlated with specific environmental conditions. Thus Crow (1924) has shown that in certain species of Blue-Green Algae certain characters which are only developed in special environmental conditions are genetically fixed in other species. In higher plants the degree of glabrousness or hairiness is subject to modification by external conditions (Warming, *l.c.*, p. 114), but in certain forms these conditions are of a fixed heredity (Bateson, 1909, p. 20). Dwarfing is certainly caused by external agencies in certain animals, and is known to occur as a fixed racial feature. Elongation of the spire of the shell in certain molluscs is correlated with specific environmental conditions, but it is known in the case of *Limnaea megasoma* to be hereditary (Whitfield, 1882).

I have met with other instances apparently analogous to the above; but they lack either satisfactory proof that the modification in question is referable to external causes, or that it has become of a fixed heredity in certain species. Thus the small fresh-water Gastropod, *Paludestrina jenkinsi*, has a non-heritable form characterised by a keel running round the body-wheel. Such a keel is a fixed specific character of *P. corolla* and other allied forms. We do not, however, know anything certain concerning the origin of the keel, though there is some circumstantial evidence (Robson, *l.c.*, and Annandale, 1924) that carination is correlated with specific external conditions.

(d) *Embryological Evidence*

The recapitulation in individual development of earlier phylogenetic stages has been explained (Macbride, 1914) as due to the inheritance of induced variation. The " tadpole " larva of the Tunicata would be considered on this hypothesis to represent a definite ancestral form which became degenerate as the result of the adoption of a sessile habit. The modifications resulting from this change became part of the hereditary constitution of the organism, and, in the course of subsequent development, made their appearance at progressively earlier stages of ontogeny until at last they became independent of the peculiar environmental stimuli that had evoked them in the first instance. Macbride (*l.c.*, p. 651) considers that " the difficulty of framing any other theory of recapitulation [than a Lamarckian one] seems to be insuperable ". I think, however, that we should distinguish between the acquisition of a new adult character or characters and the actual fact of recapitulation in ontogeny. Macbride is quite justified in raising the question whether the former may take place through natural selection or as a reaction to a new environment. The actual course of a given life-history, including the alteration of the time of appearance of any character, does not, however, seem to me to be more readily explicable on a " Lamarckian " basis than on a selective one. Gates' essay (1921, p. 81) on Recapitulation in Plants and its evolutionary significance should be consulted.

II. Experimental Evidence

(a) It is perhaps desirable to examine the experiments that have been conducted on lowly organisms such as Bacteria and Protozoa in a separate category from multicellular organisms. It is for reasons already pointed out (Chapter II.) injudicious to apply to higher organisms conclusions founded on the behaviour of the Bacteria at least. Nevertheless we ought not to exaggerate the distinction in this respect between unicellular and multicellular

organisms; in any case it is required to show on what grounds we regard the distinction as tenable.

The facts concerning the modifiability of Bacteria and Protozoa have been assembled and criticised by Pringsheim (1910), Dobell (1912), Müller (1912) and Bateson (1913). In both groups changes (both morphological and physiological in the Protozoa and physiological in the Bacteria) induced by external agencies (employment of reagents and "Tier-passage") have become fixed and permanent, though in certain circumstances (acquisition of immunity to certain drugs by Trypanosomes) it is necessary to keep the modified strain in the same environment as that in which the new character was acquired. Even in the Bacteria the latter condition is not, however, an essential condition, as Massini (in Dobell, *l.c.*, p. 329) found that a strain of *Bacillus typhosus* which had acquired the power of fermenting lactose retained that power when transplanted to lactose-free media.

That variation of this order has been induced in these organisms and that the strains thus modified breed true cannot be doubted. Bateson's suggestion (*l.c.*, p. 215) that the appearance of induced variability may be "due to the selection of a special strain living masked among other strains" is appropriate; but it seems to be rendered superfluous at least by Kowalenko's amplification of Massini's original work (cf. Dobell, *l.c.*, pp. 330-1).

If we decline to use these results as evidence in considering multicellular organisms, we should at least admit that the living substance has in these forms of life the property of retaining and transmitting modifications induced by environmental factors. That the transforming agencies (reagents of various kinds) used in these experiments are not likely to be found in the normal environment does not seem an objection of first class importance. There may be a solid reason in the separation of the germinal substance from the somatic tissues for declining to apply generalisations founded on unicellular organisms to higher plants and animals, but this is not of moment, if we suspend our judgement as to the inheritance of somatic modification in multicellular organisms and concentrate our attention on the possibility of direct modification of the germ-cells.

(*b*) The majority of the experiments which are claimed to prove that modifications of the parental body induced by various external agencies are inherited in multicellular organisms cannot be accepted as satisfactory evidence. The experiments of Ferronière (*Tubifex*), Kellog and Bell (*Philosamia*), Pictet (*Lymantria*), Schröder, Fischer, Standfuss (various Lepidoptera[1]), Guyer and Smith (*Cavia*), and Kammerer[2] (*Ciona*, *Alytes*) must be set aside or regarded as *sub judice*, either because alternative explanations of the results are available, or because the range of individual variability of the experimental animals in respect of the character under investigation is imperfectly known, or because further investigation has not confirmed the results. Pavlov's results, which seemed to indicate the inheritance of the effects of training in Mice, have likewise been contradicted by subsequent experiment (Vicary, 1924). It will be recalled, however, that so relentless an opponent of the doctrine of the transmission of induced modification as Weismann was influenced by some of Fischer's work, and found it necessary to conclude that the germ-cells can be directly modified by temperature (parallel induction) On this issue we find the evidence far more impressive.

The experiments of Tower (*Leptinotarsa*) are accepted by friendly critics (cf. Castle, 1916) with a certain amount of reservation and by others with a scepticism which is not without justification. Sumner (1915) subjected white mice to different temperatures, and found that there was an increase in the length of tail, foot and ear in the animals of the parental generation reared in " warm room " temperature. The offspring of these born and reared at normal temperature had longer tails, feet and ears than the offspring of animals kept at " cold room " temperature in three out of four lots. In the fourth the relations with regard to foot and tail were

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[1] See pp. 161-2.

[2] For the work of Kammerer on *Salamandra* and that of Dürken, see Appendix, p. 255.

reversed. F_2 animals were not dealt with. Owing to the stability of body-temperature in the adult mouse, Sumner (p. 330) does not believe that in the adult stage there may have been a direct effect on the germ-cells ; but he is disposed to believe that " the external temperature reached and modified the germ-cells " of younger animals. In spite of Sumner's arguments (p. 331), I feel that we could accept the results with more confidence if the experiments had been carried on for several more generations. Sumner also seems to treat the question of the genetic composition of his stock too lightly, and I agree with the criticism of Tower, viz., that in-bred stock should have been used.

Little room for criticism seems to be left against the work of Harrison and Garrett (1925) on the inheritance of melanism in Lepidoptera induced by the addition of lead nitrate and manganese sulphate to their diet. There is, however, a circumstance which must make us a little cautious in attributing Harrison and Garrett's results entirely to the effect of the lead and manganese salts. In the lead experiments (*l.c.*, p. 246) melanic individuals appeared in the ratio of 1 : 26 and 2 : 29 in the first broods which showed the effects of the salts. Similarly in the manganese experiments eight melanic individuals were obtained out of twenty. This seems to me a very important feature, to which the authors pay insufficient attention. Castle (*l.c.*), in discussing Tower's work on *Leptinotarsa*, comments on a similar paucity of the numbers of individuals that showed the effects of experimental conditions, and argued that the latter were merely selective, and " exerted on a collection of germ-cells already inherently variable in their potentialities ". Bateson (*l.c.*, p. 192) makes the same criticism concerning Fischer's results. I do not think that an initial difference in the constitution of the germinal material is the only possible explanation. It may happen that the adult individuals used in these experiments differed in their general physiological state. These individual differences (dependent perhaps on differences of nutrition or developmental stage) may be reflected in the cytoplasm of the germ-cells, so that the salts used in the experiments had diverse effects on such differently constituted cytoplasms with a corresponding effect on the chromatin of the germ-cells. Or the differential effects may depend on the amount of salts taken in.

Agar (1913) found that certain modifications (*e.g.* reduction of size) could be induced by high temperature in the Cladoceran *Simocephalus vetulus* and were inherited for several generations. The change, however, was not permanent. Opinions may be diverse as to the value of these results ; but it seems to me that even a temporary modification of the germinal constitution of a species is not without significance.

The suggestions concerning Harrison and Garrett's results are put forward very tentatively, and in complete ignorance of the chemical and physical changes involved in differences of pigment production and the means whereby such changes may be made effective in the hereditary material. I think, however, that the differential effect described above requires serious consideration.

Although this argument in no way weakens the case for the inheritance of an induced modification, it must incline us to believe that those individuals in which the melanic condition was produced as a hereditary character either are in a critical physiological state during which the fixation of the melanism is facilitated or carry factors which in some way co-operate in the production of the melanic condition.

Direct modification of the germ-cells by various agencies (alcohol, radium, X-rays), as well as by the infective microorganisms of disease with specific dystrophies resulting in the adult, has been amply demonstrated. These agencies are not likely to be causally concerned in the origin of normal variation ; but their effects must prepare us for similar sensitiveness on the part of the germ-cells to normal physiological change. I think, however, that the experiments of Castle and Philipps (1911) on ovarian transplants show very clearly that responsiveness of the germ-cells to abnormal environmental conditions is by no means a regular phenomenon. It will be recalled that these workers failed to obtain any alteration of the visible character of Guinea Pigs when ovaries of black females were transplanted into Albino females.

Conclusions as to the Inheritance of Induced Variation

I think the preceding survey must be held to endorse the view that we cannot as yet speak with certainty as to the origin of inherited variation. The evidence which is at all satisfactory suggests that it may be either germinal in origin or induced by external causes. In the latter case we may suspect that individual germinal differences of unknown (not necessarily automatic) origin are contributory to the change wrought by the environment. Future investigation must aim at discovering whether hereditary change can be induced by external agencies alone. Several authors have dwelt on the intimate association of the factors of inheritance and of environment in the production of new characters (*e.g.* Rabaud, 1920, p. 418), but we are not in any sense finally informed how far purely germinal change and that which is produced by the environment alone are contributory to the phenomena of hereditary variation. That they may be complementary is possible, as I have suggested above in commenting on the work of Harrison and Garrett. Many critical and carefully planned experiments must be carried out, however, before we can finally ascertain the respective importance of germinal and induced variability and their possible inter-reactions.

THE NUMERICAL INCREASE OF VARIANT INDIVIDUALS

A natural population of individuals distinguished by the possession of a heritable character not found in the ancestral stock may become established by one or more of the following processes:

(1) A new character may be simultaneously developed in all the individuals inhabiting a given area through the action of the environment characteristic of that area. (2) The individuals bearing a new character may obtain therefrom vital advantage over their contemporaries in the struggle for existence. (3) The new character may appear

simultaneously in all the members of a population through a simultaneous automatic modification of the germinal material of such individuals. (4) A few individual plants or animals exhibiting a new character not conferring an advantage upon its possessor, may find in nature an unoccupied habitat available for occupation. In this they may maintain and reproduce themselves up to the economic capacity of the habitat or area.

Actually we have very little exact information as to the origin and spread of new characters in nature. Our evidence on this subject is inferential rather than derived from observations of actual events. Substantial evolutionary change occurring in nature and in circumstances allowing continuous observation is uncommon. From Gates' accounts (1921) of the history of mutant plant-forms in nature it will be seen that *continuous* observation is rare. I do not think we can make serious use of more than two series of observations on animals—the classical study of Weldon on the modification of *Carcinus maenas* and the well-known increase of melanism in certain Lepidoptera in England and on the Continent. Other records of the appearance and spread of new variants in areas or in a stock in which they did not previously occur are known (*e.g.* in *Coereba saccharina* in the W. Indies (Bateson, 1912); in *Partula* (Crampton, 1916, 1925); in *Achatinella* (Pilsbry and Cook (1912); in *Euparypha* (Tomlin, 1927)); but the data are not sufficient for us to form a conclusion as to their significance.

(1) The Massive Transformation of a Population through the Effects of Local Environmental Conditions

Although this may be held to be proved in the case of the "industrial melanism" in Lepidoptera, and though various authors have invoked it as a chief principle of transformation (cf. Berg, 1925), I consider that, regarded as a factor in evolution, it raises certain difficulties.

By "massive transformation" I mean the wholesale modification of a large part of a population by a change which takes place in some factor or factors of its environment, as opposed to the production of a few variant individuals by the same cause and their subsequent multiplication by causes indicated in (2) and (4). No radical distinction between the two main types is involved, except that in the second case we must supply some satisfactory mechanism for the spread of a few individuals and their offspring. " Massive transformation " is often witnessed in small local assemblages exposed in special environmental conditions, and is sometimes recorded as taking place on a large scale. Unfortunately, except in the melanic *Lepidoptera* above mentioned, we have no knowledge of such transformation that is hereditary. It must be borne in mind that the spread of variants of this nature beyond the scene of their transformation, *i.e.* into areas in which the transforming factors of the environment are no longer operative, has to be accounted for. As long as each species, variety or race occupies a separate locality or habitat, there is no need to consider this, at least if we believe that each species is thus conterminous in its distribution with the environmental factors that gave it its special attributes. When, however, the areas or habitats of allied species overlap or are conterminous we cannot avoid assuming, if we wish to maintain that the hereditary characters of species and races may be induced by the factors of the environment, that the species in question arose in localities remote from one another and having a different ecological character, and subsequently spread until they met and overlapped each other. In making this assumption we have to account for (*a*) the means whereby species spread, and (*b*) the lack of local (*epharmonic*) convergence seen when structurally distinct species occupy the same or overlapping areas. We have then to consider seriously the other means of multiplication, not only of such individuals as bear characters due to purely germinal change, but also those which receive them from their environment and ultimately invade territories in which the causative factors are absent.

I do not claim that this objection is in any sense fatal to the hypothesis in question. It is possible, for example, that a variety produced by environmental stimulus might spread beyond the area over which the latter is operative, because it was better adapted or because in the adjacent territory there was available food and little competition. All I wish to point out is that this matter is completely unexplored by those who believe in mass-transformation by the environment, and until it is seriously considered we must reserve judgement as to the value of the latter.

(2) Natural Selection

Before we proceed to examine the evidence for the intervention of Natural Selection in the processes of evolution, it will be convenient to discuss what antithesis there may be between that hypothesis and the results of genetic study. As I have already stated, this antithesis is regarded by some authors as unimportant. A clear statement of this view is given by Babcock and Clausen (*l.c.*, p. 286), but, as far as the general validity of either hypothesis in giving an acceptable account of evolutionary change is concerned, that statement requires some amplification.

In the first place, the original theory of Natural Selection involved the assumption of continuous variability. In opposition to this view the earlier geneticists adduced the evidence for discontinuous change. There cannot be much doubt now that the importance of the latter was much overrated. The evidence that large discontinuous steps are frequent enough to be of importance in evolution is held to be inadequate, and there is to-day a justifiable tendency to extend the meaning of " mutation " to any change in the hereditary factors, whether it be large or minute. The revelation of the extremely complex factorial basis of many characters renders it likely that the expression of such characters may be modified by very slight factorial change, and that, as Babcock and Clausen state (*l.c.*), " mutation produces those small inheritable differences logically required for the explanation of adaptation through Natural Selection ".

The original reason for maintaining any distinction between Natural Selection and " Mutation " seems, then, to be devoid of value. With the admission that genetic research has deprived the older selectionism of its unlimited fund of continuous variation by the proof that much fluctuating variation is non-heritable, the distinction based on the size of germinal change is otherwise shown to be unreal. Moreover, there is a tendency at the present time for geneticists to admit that the survival and multiplication of a new mutant type is governed by its selective advantage (Morgan, 1926, p. 1077). Morgan (*l.c.*) has explained the relation between the results of genetical research and Natural Selection. While emphasising the erroneousness of the belief " that selection can go on changing a group as long as the process [*sc.* of selection] continues ", and pointing out that selection comes to an end unless new mutations arise, he admits that " the probability that evolution has taken place by the selection of chance variations is as great [to-day] as at the time when Darwin advanced his theory of Natural Selection ".

It seems, then, that any maintenance of a separate doctrine of evolution by mutation is scarcely justifiable, if we are to take Morgan's opinion as representative of a large body of opinion, as I think we may.

Nevertheless it may be felt that the actual incidence of Natural Selection is still imperfectly known, that we cannot guarantee that mutations, large or small as they may be, are actually preserved and accumulated by its action, and that it is possible that such variants may persist and even multiply without adventitious aid. It may likewise be believed (though this is of secondary importance) that many new characters may arise through new combinations of pre-existing factorial material.

In considering these questions I shall use the term *Chance Mutation* simply as implying the origin of any heritable difference, and later on (p. 219) I shall consider whether individuals carrying such characters can survive and multiply if they have no selective advantage. As I have indicated this is subject to general doubt, but the question requires examination.

Although the hypothesis of Natural Selection supplies an explanation of the numerical increase of individuals bearing a given character, in the minds of a good many biologists there exists a doubt not whether Natural Selection as described by Darwin and his followers is actually operative, but whether it can bring about such divergence as we see between allied species. While no one doubts that unless an animal or plant is adapted to its environment it cannot survive, it is believed that the majority of small hereditary differences are without significance in the struggle for existence. Substantial and well-marked differences, such as frequently characterise the genera and families of the systematist, may be of adaptive value ; but it is held that the initial stages of divergence, as we see them in the differences between related species and varieties, are passed through without any reference to their utility. The value of Natural Selection, as the prime cause of such divergence, depends on the utility and survival-value of these differences, and I propose to examine this question in detail.

The evidence that Darwin obtained from the history of domesticated breeds and the success of artificial selection has been regarded as inadmissible in any argument as to animals in a state of nature. It is pointed out that the success of the practical breeder and the agriculturalist has depended on pedigree-breeding and the continued introduction of fresh hereditary material into their stocks, and that fresh factorial combinations are thus set up, which allow the breeder far more opportunities of changing the character of his herds or crops than are available in nature.

It may be argued with some reason that a similar process takes place in nature, as different species are sometimes fertile *inter se* and may be often in regular contact with each other. When, however, we think of the variety and effect of the forces that procure isolation in nature (Chapter V.), it is not at all likely that such crosses will be frequent enough to provide results comparable with those produced by the husbandman. Nevertheless, in a natural population containing very diverse genotypic elements which are not segregated very rigorously and when opportunities for interbreeding are numerous, there is no doubt that at least an approximation to the genetic diversity produced by the husbandman must be attained.

If the analogy between Natural and Artificial Selection is on the whole not of prime importance because the material upon which selection is exercised is dissimilar in the two cases, it is reasonable to ask whether continued selection of *unmixed* stock produces in experiment the results assumed to result from Natural Selection. Before we deal with the actual results obtained it must be stated that, though many experiments in this sort of selection have been undertaken, only those in which selection has been sustained over many generations can be taken as evidence. In discussing their work upon selection of the " bar-eyed " mutant of *Drosophila melanogaster*, Zeleny and Mattoon (1915) make the following distinctions in the interpretation of their results. Positive results from selection may show that : (1) the factor or factors responsible for any character may be themselves variable ; or (2) that the experimental stock is not homogeneous, so that selection applied to such material may simply sort out various pre-existing factorial combinations. In order to be certain that a positive result is not merely due to the second condition, experiments ought to be continued for many generations.

The limits of experimental selection were shown by Johannsen in his well-known pure-line studies, and similarly negative results have been obtained by Ewing (1916), Jennings (1910), Ackert (1916) and others. On the other hand, Banta (1921), working on the light-reaction time of *Daphnia*, obtained a positive result in one strain out of sixteen, and Jennings claims similar results in *Difflugia corona*, though the latter are criticised by Morgan (1919, p. 207). The exhaustive studies of Castle (1914) on the amplification and reduction of the hooded pattern in rats by selection were originally held by their author to indicate a fundamental variability of the factors involved. In 1919, however, he modified his opinion, and stated that " What has really happened in the case of the selected races was more largely due to residual heredity than to any change in the gene for the hooded character itself . . . my critics have been wrong when they insisted that selection could not change racial characters which mendelise and change them permanently. . . . But [they were right] when they insisted that evidence is wanting that change in single genes occurs other than spontaneously, uninfluenced by systematic selection " (1919). We must infer from this that his later experiments (in which he crossed the forms produced by selection back to the wild (unmodified) race), led him to believe that, though selection actually did bring about a change in the colour-pattern of his experimental animals, the change wrought by selection was not a complete modification of the gene for the character undergoing selection. The grounds for this conclusion seem to be that on crossing the selected races back to the wild, he obtained a clear-cut segregation of the " wild " and " selected " factors, and not a progressive diminution of the amount of hoodedness and non-hoodedness produced by selection. I may err in interpreting Professor Castle's conclusions ; but, if I am correct, they do not seem to be in serious opposition to the views on the effect of selection which are stated below. It should be noted that the variability of the stock under selection had not diminished during twenty generations.

I do not think that the failure in certain cases to produce new strains by artificial selection can fairly be taken to prove that selection is always incapable of having a positive effect. Certainly there are several instances where negative results are obtained ; perhaps they are more frequent than positive ones. This may incline us to believe that in nature selection is equally limited in its activity. But it does not rid us of the strong theoretical presumption to which appeal is made quite frequently by the geneticist (cf. Bateson, 1909, p. 289), that if a variant of survival-value does arise it will be preserved. The negative results frequently obtained must prepare us to believe that selection is not immediately operative in all times and in all cases. That is all that we are entitled to deduce from the results of selection experiments. On the whole it seems better to assume frankly that if new variants appear in the material under selection these may be points of departure for fresh modifications. It is obvious that, if no such germinal variations arise, selection cannot alter the character of a population ; while, if they do arise, selection of the kind employed in these experiments will be effective. This admission, however, does not go to the root of the matter. The crucial question is whether there is any process in nature comparable to the selection practised by the experimental and practical breeder. No one would deny that, if a structure is definitely of service to the organism which bears it, it may be of survival value. What we have to decide is whether the differences which characterise allied species are likely to be of such value as to give their possession an advantage over the rest of a population.

In the following pages we shall mainly be concerned in examining the adaptive value of single structures and parts. A reasonable objection may be lodged against this procedure. It has been often contended (*a*) that very many interspecific and intervarietal differences are not in themselves useful, but are influenced by correlation with useful differences, and (*b*) that individual organisms are not selected on account of single differences of adaptive value, but for a general " all-round " superiority.

(*a*) Evidence will be supplied in Chapter VII. that correlation of one kind or another may theoretically at least be a means whereby non-adaptive characters have spread in a population ; but (1) we are in fact lacking in objective evidence as to the frequency of the right type of correlation ; (2) there is, as far as I can ascertain, only one very dubious instance on record (Crampton, 1904) in which a selective death-rate has influenced the other characters of a stock correlatively ; and (3), even if many differences in structure may be brought about by correlation, we must nevertheless show that some differences at least are of adaptive significance. (*b*) As for " all-round " superiority, I think we may grant that this is of importance. An organism that is well adapted to meet one type of crisis or environmental stress may not be equally able to cope with another. But " all-round " superiority must consist in a number of individual factors, so that we must inevitably study the latter before we can discuss the general fitness of the organism for its environment.

It is sometimes suggested that Natural Selection is periodic in its incidence, and that the value of a structure is not necessarily to be judged by the immediate set of circumstances in which its owner happens to be living when we have it under observation. It is possible that this may be true; but we are not thereby relieved of the necessity of finding the critical circumstances in which the structure is presumed to be of survival-value.

The apparent lack of direct utility of so many of the small differences of size, shape and colour-pattern between allied species has always been met by the advocates of Natural Selection from Darwin onwards by the argument that it is impossible to prove that a character is not of value until the habits and life-history of the organism that possesses it are exhaustively known. The force of this argument must be admitted ; but, as has already been pointed out (Richards and Robson, 1926), " the adaptive value of a structure must not be presumed in default of evidence to the contrary ". If no large body of positive evidence is available to settle this question one way or another, we are logically driven either to adopt a position of suspended judgement, or to make the most reasonable inference that is available on general grounds. It is perhaps as well to remember that Darwin himself expressed a certain measure of reserve as to the efficacy of Natural Selection. In addition to a belief in the effect of climate and nutrition (1859, p. 105) and the results of correlation, he held that some of the differences between species were devoid of adaptive significance. These " would not be affected by Natural Selection and would be left either as a fluctuating element, as perhaps we see in certain polymorphic species, or would ultimately become fixed owing to the nature of the organism and the nature of the conditions" (*l.c.*, p. 98). Nevertheless, it is by its capacity to assign an undoubted survival-value to the differences between species that the effect of Natural Selection in the initial stages of divergence must be judged.

In most, if not all, the discussions on the adaptive value of the characters which distinguish species the differences in structure are almost exclusively considered. The origin of differences in habits, of physiological constitution (including reproductive affinity), of the choice of food and habitat, are very rarely considered, and yet it is plainly part of our task to explain their origin, and, if we are to believe that Natural Selection is a general cause of all divergence, to apply that principle to them.

The origin of differences in metabolism, in reproductive affinity (sterility and incompatibility), and in special activities such as the secretion of poisons, of which we have seen some examples in Chapter III., is very obscure. It was seen there that such distinctions are by no means as definitely specific as the differences of structure, though our knowledge of this matter is not very far advanced. There is, however, enough evidence for interspecific differences of this order to make it necessary to consider the matter. Many of these differences may perhaps be considered to result from change in habits and mode of life. Observations on domesticated and captive animals have revealed alteration in metabolism and reproductive capacity, and it is likely that some of the differences described in Chapter III. may be referred to alteration in diet and other vital conditions resulting from changes in habit. But we must be able to prove that this is actually true in particular instances, and even so we are still left with the responsibility of accounting for the origin of new habits. In any case we can only refer the acquisition of interspecific sterility to changed conditions with the greatest reserve; for many species having different habits and modes of life are known to be fertile *inter se*, and others which at least appear to have identical habits are sterile. A change of habit or mode of life, whether it be an "occupation" like food-getting or the customary occupation of a special area or habitat, may arise, I think, in one of three ways: (1) it may be imposed on an organism by a change of external conditions, (2) it may be gradually acquired if a plant or an animal is driven into a new area by stress of competition, or (3) it may arise spontaneously.

It is extremely difficult to find any satisfactory proof that slight variations of this sort are gradually selected in the circumstances required, viz. pressure of over-population or change of external conditions. There are recorded instances of change of habit among animals (*e.g.* Darwin, 1859, pp. 220-21; Gulick, 1905, pp. 59, 67); but the circumstances in which the change takes place are usually unknown, and we cannot show that the change was not purely spontaneous.

Darwin (*l.c.*, p. 220) considered that it is "immaterial for us whether habits generally change first and structure afterwards; or whether slight modifications of structure lead to changed habits; both probably often occur almost simultaneously". I do not think we can regard the matter as immaterial until we know more about the actual origin of habits.

The doctrine of Natural Selection and Lamarckian argument do not require as an absolute condition that the acquisition of a new habit should precede a structural change; though, speaking broadly, both theories would be easier of acceptance if this condition were fulfilled. On the other hand, if we could produce a large body of evidence that substantial structural change regularly preceded change in the appropriate habits, these theories would not be seriously compromised, but there would be grounds for suspecting that structural change may be less dependent on environment and adaptation than is assumed by these theories. However, the mere citation of structural divergences which are unaccompanied by those of habitat and of modification of habit without corresponding change of structure are actually of little value as evidence, unless they are supported by experimental or precise knowledge of the history of the case.

The gradual and side-by-side change of structure and habit envisaged by Darwin depends on the coincidence of simultaneous variation in the two respects. I do not maintain that this is likely to be very rare ; but when the acquisition of a new habit involves much readjustment, structural and physiological, we draw very liberally on the power of coincidence !

With regard to certain habits such as those connected with mating (display, and other forms of incitement), when these are differentiated specifically, it is not at all easy to explain their origin on a selective basis (cf. p. 216).

Observations on the utility of differences in structure can be more profitably discussed, and such evidence as is available may be conveniently arranged in two classes. In the first place (A) we may deal with the correlation of structural differences with appropriate differences in habit and mode of life, and in the second place (B) we may examine the evidence for the accumulation of small structural differences by a selective death-rate observed in nature.

(A) *Structure and Habit*

The intensive study of habits and general mode of life has shown that many differences in structure and arrangement of parts which seem devoid of utility have an important rôle, and can be sufficiently correlated with differences in habits, etc. This has been shown by Garstang (1897) for the filtration apparatus of Crustacea ; by Rousseau (1926) for the structure of torrent-dwelling larvæ of Insects ; and by Swynnerton (1926), who has demonstrated the utility of eye-spots in Lepidoptera by practical tests. What is certainly not apparent in the above-cited cases, is whether differences between species as opposed to genera and larger groups are of this status, and are regularly accompanied by the differences of habit, etc., necessary to give them an adaptive significance.

It is a curious feature in the history of evolutionary inquiry that, although the selective value of slight differences between species and races has been largely assumed or vigorously denied, the question has never been systematically explored. In many works on Evolution the subject receives but superficial attention, many authors simply contenting themselves with the citation of a few ambiguous instances of some apparently unimportant part of an organism that has been shown to have some use, no mention being made as to whether the possession of such a structure differentiates one species from another. After the dogmatic assertions and denials made by evolutionists of the past, we are at present in the position of having to make the unheroic admission that interspecific differences seem to be of adaptive significance in some instances and not in others. It is desirable, however, to discover whether adaptive differences of this order are of common occurrence or exceptional.

A question deserving attention and very rarely discussed is involved in what we may call the " fit " of an animal or plant into its environment. It is sometimes assumed that adaptation need not be expressed in a rigid correspondence of structure and bionomic peculiarity. This is no doubt true; but I think we ought to be as much on our guard against an easy acceptance of this principle as against demanding an absolute correlation of structural and bionomic divergence.

Records of differences between species, varieties or races that are to be explained by reference to known differences of habit, habitat, etc., and can be called " useful " in relation to such differences are by no means easy to find. When we set out to look for such differences we most usually find very ample evidence for adaptive differences between families, groups of genera within families, and between single genera. A very good example of this is seen in the work of Lucas (1897) and Gardiner (1925) on the adaptive modification of the tongue in Birds. Gardiner distinguishes eight different types of tongue, which correspond with different modes of feeding known to be distinctive of the various families and genera. When, however, we take up the study of the species of a single genus and attempt to account for the differences between them by reference to their habits, we most usually encounter the preliminary difficulty that the habits are either not known at all or not sufficiently known to warrant discussion. To show that differences in a given structure, *e.g.* the radula of a snail, or the jaw of a mammal, are or are not correlated with differences in diet, we should require a very intimate knowledge of the food and its constituents. I think this is known in very few cases ; or, if it is known, the range of variation of the structure in the species under consideration is uncertain.

As we are to concern ourselves with interspecific and interracial differentia, it is only right to recall what was said in the earlier chapters concerning the nature of taxonomic differences. The evidence presented there concerning plastic responsiveness must make us cautious before we conclude that every and any distinction proposed in taxonomic literature is of a fixed heredity. Even if the upholder of Natural Selection is unwilling to grant that some interspecific differences may be of environmental origin and of a fixed heredity, he will rightly claim to be relieved of the necessity of explaining on a selective basis the origin of many purely somatic differences, which may be produced by the factors of the environment.

In discussions on the adaptive value of interspecific differences the importance of the question raised in the last paragraph is not sufficiently realised. Having alluded in the earlier chapters (I. and II.) to the basis of specific diagnosis, and realising (*a*) the paucity of material on which the systematist sometimes creates his species, and (*b*) the probability that many species described in systematic literature may be " environmental forms ", we must be very cautious before we saddle the theory of Natural Selection with the duty of finding an adaptive explanation for every difference recognised by the systematist as specific. At the same time we should likewise be chary of adaptive explanations of structural differences that are quite likely to be due to responses to differences of environment. Thus Plate (1913, pp. 120-2) assumes far too readily that the differences described by Woltereck between two races of *Daphnia longispina* inhabiting two different but adjacent lakes, " müssen also entweder selbst vitale Bedeutung haben oder korrelativ mit selektionswertigen Eigenschaften verknüpft sein ". Bearing in mind the structural differences that are produced by differences of environment in Cladocera (p. 173), and in the absence of direct proof of the adaptive value of the characters under discussion, we may as reasonably attribute the differences described by Woltereck to some difference in environment. A study of several admirable works on animal ecology (*e.g.* Thienemann, 1926; Hesse, 1924) will readily convince us that many interspecific and interracial differences are to be noted between the animals inhabiting different types of habitat (cf. also Chap. IV.). Some of them may be undoubtedly adaptive, but they are not all to be accepted as such on their face-value.

I think it would be right to accord the first place in an inquiry of this sort to the subject of Mimicry. The data that have accumulated on this question are now extremely copious, and it seems to me that they are in need of systematic treatment and of a more summary and concise statement than has been attempted. As Myers and Gale (1926, p. 432) state, " the subject of Mimicry [*i.e.* the views as to the interpretation of the facts] is rapidly approaching an *impasse*, and the same facts are used to support different views ". Although it is seen best in the Lepidoptera, the phenomenon is of course encountered in many other groups, in which many singular instances are known, *e.g.* between Ants and Spiders (Myers and Gale (*l.c.*)).

There can be no denial of the amazing similarity that is found between many Lepidopteran models and their mimics. The question we are immediately concerned to answer is whether the bionomic nexus demonstrated in any case of mimicry is of such a nature as to render an adaptive explanation of such resemblance the only possible one.

Within the last twelve years, the subject has been reviewed afresh from different standpoints by Punnett (1915), Longley (1917) and Carpenter (1920). The former, while not denying the close resemblance between mimic and " model ", suggests that the evidence as to the discrimination between various types of Butterflies as distasteful or acceptable is most insecure. We ought not to conclude that these remarkable resemblances are adaptive, except in the presence of completely convincing evidence that (*a*) the " models " are unpalatable, and (*b*) that they are regularly rejected in nature. However, the resemblances themselves, and the circumstances in which mimic and " model " are distributed, are too singular to be left without comment. Punnett (*l.c.*), who allows that Natural Selection may bring about the survival of those forms which happen to resemble species protected by their unpalatability, attempted to find an explanation of the origin of similar variations in species often distantly related. He suggests (p. 148) that (in Insects) colour-pattern is dependent on definite hereditary factors, of which the total number is by no means great, and that, as many of the factors are common to various groups of butterflies, certain of the patterns produced by such factors in combination should be paralleled in other groups. This suggestion is supported by other observations on the occurrence of parallel series of variants (cp. Vavilov, 1921). The resemblances between members of remote families and even orders must make us sceptical as to this hypothesis ; but I think we require to know a good deal more about the incidence of homologous series of variants before we can assert that the above-mentioned extreme instances could not have been brought about by this means. No one would suggest that our common Rams-horn Snail, *Planorbis corneus*, a Pulmonate Gastropod, is mimicked by the Nilotic Prosobranch, *Marisa cornu-arietis*, and yet the resemblance between the shells is incredibly close.

I am inclined to attach less importance to Longley's (1917) suggestion that the resemblance is due to environmental convergence, for the following reasons: (*a*) There is no evidence that the local mimetic polymorphism, such as that described by Carpenter (1920) in *Pseudacraea eurytus*, is to be associated with environmental difference alone. (*b*) It is hard to understand why such local convergence should, if due to the environment, have such a marked incidence in isolated groups, and not be of general occurrence.

The justification of the view that mimetic resemblance is brought about by Natural Selection must be mainly judged by our information as to the amount of discrimination exercised by natural enemies. The evidence that the areas occupied by mimics and models are conterminous, that they habitually live and feed together, that the relative proportion of numbers is consonant with the theory of protective resemblance, is highly significant but not critical.

Since Marshall's classical paper (1902) much evidence has accumulated on the power of discrimination exercised by Birds, Primates, Mantids, etc. Perhaps the most illuminating is that collected by Swynnerton (1916, 1926), though it is not presented in a systematic way so that one can readily determine how far mimetics and their models are involved. Swynnerton's methods and results are criticised and defended with great fairness by their author. There is no doubt that observation and experiment on captive birds is rather an insecure method (cf. Swynnerton, 1916). Nevertheless, there is a certain regularity of rejection and acceptance of certain types which is impressive.

At present there is no doubt (1) that Birds and other potential enemies do distinguish between certain types at sight, (2) that models and their mimics are sometimes thus rejected (Marshall, 1902), and (3) that sometimes a model and a mimetic female are rejected at sight, while the non-mimetic male is accepted and eaten (Swynnerton, 1926, *Charaxes cithaeron* and *ethalion*). On the other hand, I do not think it unduly captious to point out the following limitations to our knowledge of the effect of discrimination. (*a*) Exact observations (those on Birds) are limited to comparatively few species. Swynnerton's best series are confined to four species (1916) and two species (1926); it is therefore uncertain how far the total avifauna of a given area would deal with the Lepidoptera of that area. (*b*) Pertinent to this criticism is the fact noted by Swynnerton (1916) that while Bulbuls have a "low preference" for Pierines the Drongo has a high preference for them. (*c*) Although Swynnerton attempted to control the disturbing element presented in experiment by variation in the degree of hunger of the bird with which an experiment was conducted, there is no doubt that, as he himself observes,

" it does not require starvation to make a bird eat Danaines and Acraeines " (distasteful forms, *l.c.*, p. 211). Models and mimics are sometimes rejected, sometimes eaten (*Charaxes cithaeron* (*l.c.*, pp. 237, 238) ; *Dardanus hippocoon* (p. 234)). (*d*) Sometimes the basis of rejection is obscure. Forms such as the Acraeinae are plainly distasteful. But some of the rejected *Charaxes* are not (Swynnerton, 1926), and rejection is here regarded as due to general " unmanageability ". But it is not evident that the *C. ethalion* male, which is readily accepted, is any more " manageable " than the female and the *C. cithaeron*, which the female mimics, and yet both the latter are rejected.

One would, in short, say that the adaptive significance of differences having a basis in mimicry is in general supported by the ascertainable bionomic facts, but that we do not yet know with what precision selection works, and whether it is capable of bringing about the exact and highly localised mimetic relationships sometimes noted.

Let us grant, for example, that some of the remarkably close cases of resemblance, such as that described by Carpenter (*l.c.*), might be brought about by this means. In any case, this must argue a very remarkable capacity on the part of a Nymphaline for throwing the same variants as an Acraeine. When model and mimetic are closely allied, such parallel variation is of course likely. The less allied they are, however, the more desirable does it become to inquire into the general capacity of distantly related organisms for producing identical variants. It may seem sufficient that such variants are produced. Nevertheless, one may be pardoned for expressing a doubt whether normal variation, even if aided by selection, can be brought to such lengths.

The colour types found among the eggs of parasitic Cuckoos seem to constitute another satisfactory instance of such a correlation of structure and habit as may justify an adaptive explanation of interspecific differences. The copious literature on this subject is assembled by Jourdain (1925) in a valuable paper.

It is now well known that, while the resemblance between the eggs of the Cuckoo and those of the foster-parent may not be close and is sometimes absent, nevertheless the eggs of a single species of Cuckoo may attain a high degree of resemblance to those of several foster-parents (cf. *C. canorus telephonus*). As the difference between, *e.g.*, the eggs of a pipit-cuckoo and a wagtail-cuckoo are correlated with the difference in foster-mother, the probability is that the resemblance between the pipit-cuckoo's eggs and those of the pipit are brought by the ejection or desertion of all cuckoo eggs that do not resemble those of the foster-parent. What is not yet apparent is whether, when resemblance is very marked, there is evidence of acute discernment and rigid selection by the foster-parent. This is discussed by Jourdain (*l.c.*, p. 652), who says: (1) The proportion of rejections by the fosterer (either by desertion or actual ejection) varies very considerably, and (2) the rate of rejection is not necessarily connected with the closeness of the mimicry. Observers simply assume at present that when the cuckoo's eggs do not resemble those of the foster-parent, as, *e.g.*, in the case of the Hedge Sparrow and the African Bulbul, the foster-parent is deficient in colour-perception! However, it is very difficult to see by what means the resemblance is brought about, if selection is not the transforming agency.

Having thus considered two series of phenomena in which an adaptive explanation of the differences such as are usually found between allied species seems to be the most likely, let us now proceed to examine some other instances of interspecific differences which may be correlated with significant differences of habit. In this second series the proof of the necessary correlation of habitudinal and other differences with those of structure are not so complete as in the previously considered data.

(1) Annandale and Hora (1922) state that in the fish, *Glyptosternum andersoni* and *G. feae*, the lips are comparatively small, while in *G. labiatum* and *G. blythii* they are more highly developed and function as suckers. The same differences are found in the tadpole of various Batrachians. " In both these groups the evolution (of

species with more efficient oral adhesive organs) can be correlated with life in waters of stronger and stronger current."

(2) Hewitt (1914, p. 11) has recorded that the lizards, *Typhlosaurus lineatus* and *Typhlops schivri*, which live in the more arid parts of the Kalahari Desert, are both separated from their allies by the possession of a sharp cutting snout, which enables them to burrow in the sun-baked soil of that region.

(3) The same author (1918) states that certain species of South African scorpions (*Opisthophthalmus*) which burrow in sand are distinguished by the possession of highly granular sternites, which Hewitt considers are of use in burrowing in sand. The correlation is not absolute, however, as forms with smooth sternites are sometimes found burrowing in this kind of soil.

(1) to (3) are of the nature of casual field notes rather than extended and intensive studies of the correlation of habit and structure.

(4) Among the parasitic ticks of the genus *Ornithodorus*, Nuttall (1911) has shown that there is a more or less distinct gradation in the degree to which the hypostome (organ of adhesion) is covered with teeth. Thus in *O. megnini*, which remains attached as a nymph for a long time, the hypostome is completely and heavily toothed ; in *O. vespertilionis*, which is attached for a few days, the dentition is less developed, while in *O. moubata*, which feeds very rapidly as a nymph, the dentition is still more reduced.

(5) Lutz (1908, pp. 17-21) has considered the length of the ovipositor in the common crickets (*Gryllus*) of America in relation to the soil in which they deposit their eggs. He points out that on a sand-spit in Cold Spring Harbour the ovipositor of crickets which place their eggs in sand is somewhat longer than that of the forms which deposit them in denser soil. He considers that the eggs deposited in sand are more liable to be uncovered and destroyed than those placed in the denser soil, and that the longer ovipositor is able to excavate a deeper hole for this purpose. He shows

that, *e.g.* in *G. arenaceus*, a sand-loving species, the ovipositor is long, and that Uhler found that in *G. pennsylvanicus*, which lives on loamy soils, it is short. Differences of unknown significance in the tegmina and wings accompany the change in the ovipositor at Cold Spring Harbour. The difference between the mean length of the ovipositors of crickets living in the sandy apex of the spit and in the mainland humus is 2 mm. This instance seems to be satisfactory, though I am inclined to think that a mean difference of 2 mm. is hardly likely to provide sufficient extra depth to be of much account. One would also like to see some verification of the assumption that eggs buried in the sand at the apex of the spit are uncovered and destroyed, unless they are deeply buried.

(6) C. Boettger (1921, p. 321), as the result of a study of the relations between carnivorous beetles, *Carabus*, and land-snails of the genus *Otala* in Morocco and Algeria, concludes that there is a reciprocal modification of the head of the beetle, *Carabus morbillosus*, and the shell of the snail, *Otala tigri*, on which the former preys. *C. morbillosus* thrusts its head into the aperture of the snail's shell to attack its prey, and as a defence against this the aperture is provided with a jutting tooth, which partly closes the aperture. In those areas in which *O. tigri* and its allies are provided with progressively larger teeth, the Carabids develop narrower heads, which should enable them to penetrate past the tooth. This relationship of attack and defence would be better established if Dr. Boettger had shown that, in areas in which the Carabid is absent, the snail does not exhibit the tooth, or that such teeth (which occur in other genera) are only found when snails are preyed on by enemies having the appropriate habits.

(7) In the rivers of Albania and Dalmatia, there is found a small fish, *Salmo obtusirostris*, which differs from the common Salmon parr in having a smaller mouth, weaker teeth and more numerous gill-rakers on the lower part of the first gill-arch. According to Regan (1925, p. 5) the difference in the number of gill-rakers, the mouth and teeth is related to a difference in diet between these fish.

S. obtusirostris feeds on larval Ephemeridae, and the size of the mouth, etc., of the Salmon parr is related to the fact that as an adult it feeds on larger organisms. As Regan points out, piscivorous fish, such as the pike, have a few rakers of insignificant length, while plankton-feeding fish have numerous and long ones. There is thus a good preliminary case made out for a relation between diet and the number of rakers.

(8) Schmidt (1917) has shown that in the upper reaches of the Danish fjords the average number of vertebræ in the Blenny *Zoarces viviparus* is 109-108, while at the mouths of such fjords the average is 115. Regan (*l.c.*, pp. 6-7) has suggested that this decrease in number is related to the diminished activity of the fish in the quieter conditions of the water of the fjords; for, as a general rule, the fish of rapidly flowing streams or of water subject to agitation tend to have more vertebræ. There is as yet no proof that the fish in the inner parts of the fjords are less active, or rather that the conditions in the latter call for less activity than the levels at which *Zoarces* habitually swim at the mouth of a fjord.[1] Regan, however, suggests that the food supply is more plentiful in the inner recesses of the fjords, and, presumably, that there is less call on the swimming powers of the *Zoarces* in obtaining food. It will be recalled that variation in the number of vertebræ has been referred by Berg in a rather vague fashion to the direct influence of the environment (p. 162).

There are possibly other more satisfactory instances in which slight differences of structure of the type here described may be related to differences in habit, " occupation " or the vital needs of species, but I have not succeeded in finding any more conclusive than those set forth above. The structural differences between the various species of a genus which can be without hesitation explained as adaptations to particular needs or habits seem more usually to be of a magnitude which transcends the level of species (cf. Dendy, 1916). Even between genera it is not uncommonly found that the

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[1] But the lesser activity of the fjord fish may be fairly inferred from their shorter and deeper build.

differences are of such a nature as to raise the suspicion that their utility and survival value are very problematical.

In few of the instances just described, (1) to (8), are the conditions in which the animals live exhaustively known. Allusion to control observations (employed by Lutz, *e.g.*) is not made in all instances. Nevertheless we must attach a certain amount of importance to this evidence. We may be sceptical as to the absolute nature of the adaptation or even as to its invariable occurrence ; but we must allow that at least the circumstance of the animals' lives do seem to supply a clue to the differences in structure, if not to the origin thereof. I think it would be perverse to deny that the difference between the heavily denticulate hypostome of the nymph of *O. megnini* and that of *O. moubata*, which bears less than half as many teeth and those not so long and pointed, is sufficiently correlated with the time of adhesion. When an interspecific difference is of this magnitude and is accompanied by appropriate differences in habitat, it is waste of time to deny that the utility of the structure is proved. When, however, we review the differences between the species constituting a group showing such particular adaptations we are on less secure grounds. How, for example, are we to explain the differences between the adult hypostomes of *Argas persicus* and *reflexus* (Nuttall, *l.c.*). They both represent a stage midway between the heavily armed hypostomes of *O. megnini* and the poorly toothed one of *O. moubata*. But in *reflexus* there are more teeth than in *persicus*, but smaller, and the arrangement differs in a characteristic way. Both are parasitic on common fowls and pigeons (Nuttall, *l.c.*, p. 51). *A. persicus* seems to have a wider range of hosts (p. 48), though we perhaps ought not to assume that the exact range of hosts is known. Are we to assume that, having certain hosts in common, they parasitise different parts of the latter, a circumstance which might require a difference in the structure of the hypostome? There is no evidence on this point, and the suggestion is not very plausible. In any case I doubt very much whether in fact difference in host or part occupied does determine the form of the hypostome. A very striking support of this doubt is found in Nuttall's figures (p. 65), illustrating the sexual dimorphism of, e.g. *Ixodes ricinus*, in which the males and females found *in copula* on the same host have markedly different hypostomes.

Let us take another example illustrating the stage at which the adaptive significance of relatively slight differences becomes apparent. *Hexalebertia complexa* and *Pilolebertia insignis* are two fresh-water mites, the one inhabiting rapidly flowing streams and springs, the other living in ponds and lakes. According to Thienemann (1925, p. 61) all invertebrate animals that live in swiftly flowing streams are devoid of the swimming-hairs that are found on the legs of such forms as live in still water, and accordingly we find none in *H. complexa* and a strongly developed bunch of bristles in *P. insignis*. Thienemann states that these bristles are disadvantageous to the stream-dwellers, as they supply extra surface for the force of water to play upon. This would presumably lead to the animal being carried away from its normal habitat. This explanation may seem somewhat circumstantial; but let us accept it. Definite as the difference between stream- and pond-dwelling forms may be, and useful or obnoxious as the hairs may be to the one type or to the other, their presence appears on closer study to be a character of all pond forms, and the lack of them an attribute of stream forms. The distinction is between different sub-genera and genera rather than between species. The latter are distinguished by minor but quite constant differences, *e.g.* in the number of spines on the basal segments of the legs, for which no adaptive significance is suggested (Viets, 1923).

The study of a large number of similar instances has led me to conclude that the adaptive value of a structure is mainly determined after it has attained a degree of development which we usually recognise as distinguishing sub-genera and genera. The distinction between a strongly marked species and a sub-genus is of course arbitrary. All I wish to suggest is that the utility or harmfulness of a structure is established, or, to state the case less dogmatically, its utility only becomes apparent to the human investigator, when it has reached a certain clearly marked stage of development.

Having thus studied a number of single characters, for the particular expression of which an explanation has been sought in some special feature in the lives of the animals which exhibit them, it will now be advantageous to see how far it is possible to give a similar explanation for several character-differences which collectively distinguish two allied species. This discussion is an attempt to ascertain how far the various structural differences between two congeneric but tolerably distinct species may be explained by the habits and life of the animals in question as far as they are known in a single area. It is not an attempt to discover the origin of such characters. The conclusion that this character or that does not seem to be adaptive does not imply that it was not at one time of such significance. Our question is simply—to what extent are the differences now to be described adaptive at the present time and in the particular section of the population with which we are concerned. I have selected for this purpose the Brown Hare, *Lepus* (*Eulagus*) *europaeus*, and the Mountain or "Blue" Hare (*Lepus timidus*), and will confine my attention very largely to the descriptions of the forms at present inhabiting the British Isles.[1]

While it might have been advantageous to study the two species over their whole range, I have deemed it advisable to concentrate on the information available for a more limited area in which the animals have been intimately studied.

The Brown or Common Hare is distinguished from the Blue or Mountain Hare by the following characters. The coat is ochraceous or rufous, and there is no special winter pelage as in the Mountain Hare. The ears, whiskers and tail

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[1] The fact that these forms are sometimes placed in different groups or sub-genera indicates no more than that they are rather clearly distinguished from each other. I have selected them for this purpose because their habitats and mode of life are fairly distinctive and have been intimately studied for many years. In attempting a study of structure in relation to habits, it is well to select two forms about whose identity there is a minimum of ambiguity.

are longer, the eyes are less prominent, and the olfactory region is more developed. The limbs are shorter and the feet smaller. The cheek-teeth are less deeply rooted. It has six mammæ, instead of eight as in *L. timidus*, and there are sundry differences in the skull and mandible (*e.g.* the brain-case is relatively narrower and deeper). Barrett Hamilton (*l.c.*, p. 250) is of the opinion that the character of the teeth indicates that the Brown Hare is naturally a grazer on soft grassy herbage, not on coarser foods such as the stalks of herbaceous plants or bark. The longer ears and whiskers and less prominent eyes, according to him, are " probably indicative of a more nocturnal habit ", and " the fur is that of a recent immigrant from less rigorous regions ". This view is superficially substantiated by the facts that the Brown Hare is typically an inhabitant of the cultivated lowlands, and its mountain relative is more frequently found on moors and hills. As for any difference in the time of appearance, I think this can be discountenanced. I cannot accept Barrett Hamilton's view that the Brown Hare is of " a more nocturnal habit ". To begin with, it is at least in the English countryside very often seen in the daytime, and if it is perhaps more commonly seen feeding at evening it does not, according to all the authorities I have consulted, differ essentially from the Blue Hare herein. The Blue Hare is by general consent a bolder or more inquisitive animal than the Brown Hare. The diet of the Blue Hare is said to be similar to that of the Brown Hare (*ib.*, p. 323) ; but it obviously can sustain itself on lichens, heather and other tough plants. The Brown Hare by all consent (Barrett Hamilton, *l.c.* ; Millais, 1904) is very varied in its tastes, and will often eat the bark of young trees and other tough material.

The origin of the two species is obscure. *L. timidus* may be of N. American origin, possibly of Asiatic. *E. europaeus* probably originated in Central Europe. In the British Isles *timidus* is found represented by a sub-species, *L. timidus anglicus*, in the Pleistocene ; but it is uncertain when true *timidus* appeared. *E. europaeus* does not appear in the British Isles until Romano-British times. The two species may then have arisen in places remote from one another and in circumstances very unlike those in which they live to-day. We have, then, to confine our attention to the latter and to consider, (1) whether the structural differences they exhibit in the area in question are adaptive in the sense that if they did not possess them they could not live where and how they do, and (2) whether there is anything that suggests that the Mountain Hare (*a*) was progressively adapted to living in mountains by the selection of forms having certain characters, or (*b*) simply abandoned the low-lying cultivated country to its rival and became restricted in its range. It is obvious that either may have happened, and it makes much difference if we can decide whether the animal became progressively adapted to a special habitat, or whether its range was restricted in spite of its structural fitness for living in other places.

Dentition.—The habits and diet of these animals do not suggest that there is any strict adaptation to different foods which might explain the differences in dentition. They both eat very much the same range of plants, and the Brown Hare admittedly will eat bark. The Mountain Hare is probably more capable of maintaining itself on a rough diet. We do not as a matter of fact know that the Brown Hare cannot do so. In any case it is quite likely that the Mountain Hare is not specially adapted to such diet, but has merely been driven off part of its range, for it comes down to feed on lowland pastures in winter (Millais, *l.c.*; Barrett Hamilton, *l.c.*), and conversely the Brown Hare is often found in Scotland living at considerable heights and away from pasture land.

Coat Colour.—(*a*) *Summer Coat.*—The "smoky-brown" of the Blue Hare and the rufous or ochraceous colour of the Brown Hare do not seem in general to be assimilative or to afford each a special protection. Having considered the backgrounds against which these animals habitually live, Barrett Hamilton (p. 321) says, "it looks as if any shade of grey or brown must be equally valuable or valueless for protective purposes in summer". At least, as far as the Brown Hare is concerned, the movements and characteristic shape of the head and ears render the animal very conspicuous, and I can testify from personal experience in shooting this animal that, although the coat colour has a certain assimilative effect, unless the animal is crouching in concealment behind vegetation, it is invariably perceptible at least to the human eye.

(*b*) *Winter Coat.*—The white or transitional " blue " of the Mountain Hare is supposed, along with other similar cases, to be protective. In regions in which there is a heavy and persistent snowfall, this may undoubtedly be true, whatever the origin of the colour-change may be. But in parts of its range, *e.g.* in Scotland, the snowfall is not so universal or persistent as to supply a permanent winter background. In the second place, it has been frequently noted that in winter the Mountain Hares tend to migrate downwards into the valleys where they meet and mingle with the Brown Hare. There being an alternative explanation for the origin of depigmentation in Arctic and sub-Arctic animals, we should perhaps let this question rest undecided in our particular case, with the admission that, in the areas of permanent winter snow, the white pelage may be an advantage.

Ears and Whiskers.—The larger ears of the Brown Hare may have advantaged it against its enemies, as conducing to quicker hearing, while the shorter eared Mountain Hare may have given way before its better endowed rival. The ear of the Brown Hare is on the average 17·2 per cent of the total length, and that of *L. timidus* is 14 per cent (Barrett Hamilton, pp. 267 and 318). It is perhaps doubtful whether such a difference would confer a definite advantage on the Brown Hare. However, if we grant that an animal with ears somewhat larger than an allied form has an advantage, the possession of smaller ears does not in the case of the Mountain Hare seem to interfere with its well-being, as in spite of the attacks of its enemies (Crows and Foxes are said by Millais to be the more destructive) it seems to be on the increase in parts of Scotland (Barrett Hamilton, *l.c.*, p. 310). I feel that if the longer ears of the Brown Hare are to be regarded as adaptive, it should be shown that in the area from which it has driven the Mountain Hare there occurs some enemy absent from the area in which the latter now flourishes. Whether the Mountain Hare is more immune from the attacks of Man and dogs and wild carnivora in moorland than in cultivated country I cannot say. It is possible that it is thus immune; but equally possible that it is more exposed to the attacks of eagles and crows in such country.

Limbs.—It might be considered that the longer legs of the Blue Hare enable the animal to cover the rough ground of moorland and hill-side more rapidly. We do not know, however, that longer legs necessarily imply greater agility, and it is to be noted that in speed and activity the Mountain Hare is rated as inferior to the Brown Hare (Barrett Hamilton, *l.c.*, p. 319). It is of some interest to note that the hill races of British Fox ("Greyhound Foxes") are longer in the leg than the lowland "Terrier Foxes" (Anon., 1910, p. 18). This character may be either adaptive or environmental in origin

Number of Mammæ.—It is difficult to see in what sense the number of mammæ is adaptive in the two cases, as the number of young is supposed to be the same in the two forms (Barrett Hamilton, *l.c.*, p. 323).

As we have already seen that the actual origin of these two species and the conditions in which they arose are unknown, we manifestly cannot speak with authority as to the way in which the characters were differentiated. As far as their present habits and distribution in the British Isles are concerned, we can scarcely argue how far they account for the differences in structure which we have reviewed. That they occupy habitats of a different, or partly different, ecological nature is plain; but they overlap to a certain extent, and it does not seem that their habits, etc., are so clearly differentiated as to explain the structural differences. Two characters, however, seem susceptible to an adaptive explanation, viz. the winter pelage of the Mountain Hare and the difference in ear-length; though the latter must remain somewhat subject to doubt. It must be remembered that this discussion aims at presenting the structural differences between two congeneric forms in so far as they may be related to habit, etc., observed in a given area. The value of a bionomic picture of this sort is methodological, and it is not offered in support of any particular view or theory.

The general impression we gain from a study of these two animals is that in Great Britain at least the structural differences do not, with two possible exceptions, correspond to two radical differences in habit and mode of life in relation to which they have been of selective value, but that the Brown Hare has supplanted the Blue Hare very possibly on account of the boldness and more confiding temperament of the latter which, as the country was brought into cultivation and more systematically hunted over, laid it open to destruction by men and dogs.

There seems to be no active competition[1] between these animals. Millais (*l.c.*) states that he has never observed the Brown Hare driving the Mountain Hare out of any area, as the former is driven away by the Rabbit. Elsewhere other species of Hares are known to have been ousted out of their original habitats by allied species (cf. Barrett Hamilton, *l.c.*), and in the case of *Lepus americanus* and *L. campestris* this replacement is contemporaneous with an increase in cultivation of the area inhabited. But in all these instances, as in the case of the ousting out of the Black Rat by the Brown Rat, the reason for the supersession of the one form by the other is obscure.

The view that morphological differentiation is closely correlated with differences in adaptation gains apparently some support from the facts of distribution. In Chapter IV. we saw that, although not uncommonly allied species tend to occupy the same areas or habitats, on the whole they are usually found in different or overlapping ones. Thus apparently one of the prerequisites of the selection hypothesis is fulfilled. Nevertheless when we consider that (1) difference of area may not involve difference of external circumstances,

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[1] *I.e.* actual hostility. See p. 209.

and (2) that we should be able definitely to assign some at least of the structural differences between species living in different habitats to known differences in the latter, it must be granted that a general correlation between structural and distributional difference does not necessarily imply that the former is adaptive.

It is perhaps worth our while to describe some more typical interspecific differences that the systematist encounters. Very little is known concerning the intimate habits of the animals to be described ; but these examples are introduced in order to display the sort of differences for which we must supply an adaptive explanation, if they are to be attributed to Natural Selection, and the difficulties with which such a task is attended.

In the Decapod Cephalopoda the horny rings of the suckers of the arms and tentacles are beset with teeth. The arrangement of the latter, their size and shape, are very diversified, and to the systematist they are in most cases a clear guide in the discrimination of species. These teeth are no doubt of service in grasping the fish on which these animals prey, and we may believe that many of the main types are suited to tackling different kinds of prey. But as between the species of a single genus or between some related genera in which the teeth vary in clearly marked but trivial differences of number, height and spacing, we cannot believe that the differences indicate that different kinds of fishes are regularly and habitually selected for food. For example, the species of the squid *Sepiotenthis* differ principally in the number of teeth, *e.g.* one having eighteen to twenty-two, another twenty-five and so on, or the teeth are triangular in shape or more elongated. Again, the two genera of Egopsid, *Illex* and *Todaropsis*, differ in the shape of the teeth of the sessile arms, *Illex* having broad squarish teeth, with a larger median tooth, while *Todaropsis* has rather triangular pointed cusps. Our ingenuity is baffled in the search for an adaptive explanation of such differences.

In the Octopoda which inhabit deep water there is a general reduction of the width of the mantle-aperture, through which the respiratory current is inhaled. The general significance of this modification is obscure, and it may not even have in its most extreme condition any adaptive value. It is possible, however (cf. Robson, 1926), that it may serve to keep the sediment of the bottom (an omnipresent danger to deep-sea benthic organisms) from entering the mantle cavity and clogging the gills. The various species of *Octopus*, *Bathypolypus*, etc., exhibit slight but, as far as I can estimate, constant differences in the width of the mantle-aperture. While we may believe that the complete closure of the gill-chamber may be an advantage, it is highly improbable that the slight differences between allied species could arise from individual difference in adaptation.

The difficulty of proving the utility of structural differences between species emerges with clearness in certain special circumstances which must now be reviewed.

(1) Differences in a colour or a pattern, which during life is completely hidden or covered over, cannot be regarded as adaptive in the sense in which colour or pattern is ordinarily held to be of use (viz. protection, warning, sexual display). Specific differences of this kind are seen in the genus *Conus* (Gastropoda), in which the elaborate colour-patterns of the shell are covered over during life by a dense horny skin (*periostracum*).

(2) It is difficult to decide whether a given structure, which is undergoing atrophy, is actually functionless. It seems, however, that the fragile internal "pen" or gladius of the various genera of Squids can be of very little utility, either as a general support of the main axis of the body or for the insertion of special muscles. Nevertheless such structures frequently exhibit constant specific differentiation. The same argument may be applied to the internal shells of certain Pulmonate Gastropoda.

(3) It is difficult to give a satisfactory account on orthodox adaptive lines of the structure of such organisms as certain abyssal Octopoda. In the latter we find that (Robson, 1926) *in the same species* some of the vital organs seem to be adapted for life on the bottom in deep water, and others are

more suited for shallow water or surface conditions. There may be a special explanation dependent on the habits of these animals, which may show that these anomalies are more apparent than real. But a study of the evidence at present available does not encourage this belief.

(4) When allied species or varieties with well-marked differences of structure and colour live habitually side by side, we must either conclude that such differences as may occur in their structure are either of no adaptive value, or that we have neglected or are ignorant of some critical difference in the habits or life-history. It will be apparent, I think, from Chapter IV. that in no case can we speak with absolute confidence concerning the latter in the case of animals. When the habits, etc., are well known, as they are of certain species of land-snails (*Helicella*, *Cepea*, etc.), it becomes increasingly difficult to find any critical differences in habit to which we can refer the actual structural differences.

(5) Many conspicuous colours are considered to have arisen through sexual selection, and it is plain that, if this is the case, there is throughout the Animal Kingdom a conflict, so to speak, between the claims of mating on the one hand and concealment on the other. How these claims are adjusted must be considered in particular instances ; but the merits of these claims must be always borne in mind. I do not think any naturalist would be rash enough to lay it down as a general principle that adaptation works to such a fine measure that a nice balance is obtained between the two, and that conspicuous colours emerge only in the absence of the need for protection and vice versa.

(6) Another difficulty encountered in applying any theory of selection is that which arises when we seek to account for certain types of presumed protective coloration. That many species do in fact resemble their natural background very closely and that allied species and varieties inhabiting different types of vegetation and soils may differ in colour accordingly, need not, I think, be questioned. A very remarkable example of the regular occupation of territories differing in the colour of soil is given by Bannerman in his recent

account of the crested Lark of Tunisia (1927).[1] The difficulty in establishing a causal connection in terms of adaptation between the colour of soil or vegetation and that of animals which exhibit assimilative colouring arises from our general ignorance of (*a*) the habits of predaceous animals and their prey, and (*b*) the conditions in which the former seek the latter. The matter has been considered with special reference to the colour of animals inhabiting deserts by Buxton (1923, pp. 140-170), and, although some of his conclusions may be questioned, he succeeds in showing that in this series of presumed adaptations the selective explanation is beset with numerous pitfalls. While admitting " that many desert animals are rendered invisible by their colour " and that " to these forms the theory of protective coloration may rightly be applied ", he considers that the theory only covers a small portion of the facts. " It is not easy to apply it to animals which hunt or are hunted at night ; or to animals which appear to be without any large enemies more powerful than themselves, or to animals whose pallid colour extends to their bellies and the soles of their feet. It cannot be applied at all to . . . black animals " [of which there are many examples in desert faunas].

It would be merely perverse to deny that assimilative coloration may in certain instances be of advantage. The experiments of di Cesnola and Poulton and Saunders clearly show that conspicuous animals are eliminated more rapidly than those which harmonise with their background.

But when we consider the frequency with which differently coloured animals live on the same type of background (cf. Boulenger, 1920, p. 222 ; Buxton, *l.c.*, p. 146), the instances of " ruptive " and assimilative coloration among such animals as snails that live buried almost continuously from sight under vegetable debris, of brightly coloured snails that are palatable to birds, and yet expose themselves in conspicuous places, and the observations of Pearl (1911) on the lack of discrimination between differently coloured forms which is manifested

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[1] The agreement between plumage and soil-colour is, however, not nearly so close in some circumstances as in others (cf. *l.c.*, p. 98, top).

by birds, we can but conclude that, whatever may be the rôle of particular colour-differences, the need for protection or concealment cannot be systematically invoked as a cause (cf. also remarks on Mimicry, p. 189).

(7) In general the principle of Natural Selection requires some measure of difference in habit or function to be correlated with differences in the structure of an organ of known function. This is not only difficult to establish in many cases, but we are also not uncommonly confronted with anomalies. Thus identity of structure may be found associated with difference of use (Grasse, 1924, p. 469, Ovipositor of *Barbitistes*), or differently shaped structures may be put to the same use (*l.c.*, pp. 470-71).

On the evidence collected in the foregoing pages as to the correlation between structural differences and such differences in habit and " occupation " as may serve to explain the former on an adaptive basis, I think we would admit: (1) that there are certain special instances (Mimicry of Lepidoptera, Parasitism of cuckoos) in which an adaptive explanation of interspecific differences is the most likely; (2) that there are a number of " border-line " cases in which the adaptive nexus is less satisfactorily shown, but is likely to be present; (3) that there is a very large array of interspecific differentia which, when we have made allowance for those due to plastic response, either await an explanation on adaptive lines or by their very nature seem unlikely to be susceptible of such an explanation.

The evidence assembled is zoological, and I am a little uncertain how far the verdict suggested above would be acceptable to botanical specialists. The impression which I have received from a study of adaptation in plants (exclusive, of course, of individual " accommodation " (Cuénot)), in so far as I am competent to judge this matter, and from discussions with specialists, is that it is not easy to find positive evidence for the correlation of interspecific differences of structure with bionomic differences that may explain the former. Structural differences between species belonging to the same genus (e.g. *Geranium pratense*, *pyrenaicum*, *molle*, etc.) which can be explained as adaptations to cross- or self-fertilisation or to fertilisation by one kind of insect rather than another (e.g. *Epipactis latifolia* and *palustris*, Darwin, 1877) may be readily found. There seem to be many other instances, however, in which the adaptation, *e.g.* to fertilisation by various kinds of insects, is less strict and the interspecific differences are less clearly associated with bionomic differences. In any case the selective advantage of being fertilised by one type of insect rather than by several seems very uncertain. However, if we accept modifications of this sort as evidence of adaptive differences between allied species, there remains a very great variety of interspecific differences of divers kinds for which no satisfactory explanation is available.

(B) *The Action of a Selective Death-rate*

In the preceding section we have confined our attention to the differences between allied species, and endeavoured to ascertain to what extent they fulfil the general condition of utility and adaptation imposed by the theory of Natural Selection. We have now to consider the actual process of selection itself.

The proof of adaptive differences between species does not imply that such differences have been actually produced by Natural Selection. An " indifferent " character that had existed for some time without conferring any advantage on its possessor might, through some change in the life of the latter, acquire adaptive value without having been in any way influenced by selection at the offset. It is necessary to point this out, because the facts of adaptation in themselves are sometimes adduced as evidence of selection. We may, if we accept this suggestion, get over the difficulty so frequently alluded to of explaining on an adaptive basis the preliminary stages of any adaptive character, which, if they are of trifling dimensions, could scarcely be of sufficient importance to turn the scale between survival and extinction. We are not, of course, relieved of the necessity of accounting for the multiplication of individuals bearing non-adaptive characters (cf. p. 219).

I do not think we need doubt that one of the prime conditions of Natural Selection, viz. competition between allied species and between the members of a single species does exist. In the history of the Brown and Mountain Hares above recounted, it is suggested that in the course of competition the former has ousted the latter out of a given area. Other examples are to be seen in the success of the Brown Rat (*Epimys norvegicus*) at the expense of the Black Rat, of *Lepus Campestris* and the Cottontails at the expense of *Lepus americanus*, and of *Lepus americanus struthops* at the expense of *Lepus arcticus* in Newfoundland. Other examples are given by Darwin (1859, p. 93). We must not, however, assume that because one species supplants another in a given area that the successful form is victorious in virtue of the superiority of all the points in which it differs from the less successful species. Nor should we assume that the unsuccessful form, if it comes to occupy a different habitat as the result of competition, is subject to a selective adaptation thereto. It may simply be restricted to part of an originally wider range. In the case of motile animals it is not necessary to assume that the competition involves a high death-rate among the unsuccessful forms, as they may simply migrate to a fresh habitat.

Darwin pointed out (*l.c.*, p. 92) that competition will be invariably more intense between the individuals and varieties of the same species rather than between species. If we are prepared to assign an important rôle to Natural Selection, I think it is, however, by no means clear whether it is more effective through intraspecific than through interspecific competition. Whenever we visualise the steps by which a population may be transformed by Natural Selection we usually picture a process operative over many successive generations, in each of which a certain number of individuals of inferior endowment are eliminated by a selective death-rate. The latter, as Darwin pointed out, need not be regularly operative in each generation. There may be periodic relaxation or cessation of selection. This matter has recently been studied in relation to the fluctuation in the numbers of animals by Elton (1924), who has pointed out several important consequences of such fluctuation. I venture to think that those who have considered the question of intermittent selection have neglected an important result of irregularity in the death-rate.

Let us suppose that a certain population of animals is exposed to a selective death-rate as the result of which some structure or structures undergo modification. In the next generation selection may be more stringent than in the preceding one, or equally stringent, or it may be relaxed. The standard of survival (that minimum condition or expression of the character undergoing selection which qualifies the organism possessing it for survival) will vary accordingly, and the rate of modification of the character will be quickened if selection is more stringent, or be unchanged if it is equally stringent, or it may be slowed-down if selection is relaxed.[1] The rate of modification thus seems to depend on the amount or degree of competition, in other words, on the standard of survival; and, if the three possibilities stated above are regarded as tenable, then we have to admit that progressive modification is always liable to fluctuations dependent on the intensity of selection.

It may be held that the material and circumstances of evolution are ample enough for the chances of retardation arising out of fluctuations in the selective death-rate to be neglected. At least the external conditions in which selection might be operative are often known to undergo progressive change, and are likely to lead to a continuous raising of the standard of survival. Long sustained changes of climate and movements of the earth's crust are likely to produce in their train circumstances favourable to continuous and progressive selection. On the other hand, the fluctuations in numbers which have been shown to occur among mammals and are a likely source of intraspecific competition are peri-

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[1] I am unaware of any experimental work which might show whether reversion actually takes place if selection on a given character is relaxed

odic, a maximum of numbers occurring once in so many years. The periodicities so far traced range from two to twenty years (Elton, *l.c.*). In competition arising from fluctuation in numbers we would then expect not a progressive selection, but alternations of rapid selection, retardation and possibly of reversion. A selective death-rate is not only operative through the struggle for the means of subsistence and reproduction, in which struggle the question of numbers is directly involved. It may be more immediately effective as when an epidemic, bad weather, or some local disturbance in physical condition occurs. Among the latter may be mentioned silting-up of estuaries and disturbance of a coast-line. When these, which are very variable in their incidence and intensity, are direct causes of a selective death-rate, there must be frequent fluctuations in the standard of survival.

We may thus divide the circumstances, in which selection may be presumed to arise, into two main groups—long sustained episodes which are likely to give rise to progressive selection, and periodic fluctuations irregular in their intensity and likely to cause alternations in the standard of survival. At first sight it seems that the former are only likely to be operative on ultimate analysis very occasionally, *e.g.* during earth movements and climatic changes of very great magnitude. When we consider the history of the British Isles, for example, since the Quaternary with its frequent oscillations of level (local and general), it seems in this case at least that the greater part of the changes to which animals and plants have been subjected is not sufficiently sustained to allow of progressive selection. We ought not, however, to assume too readily that the oscillations that are perceptible in climate and level of the earth's surface preclude any sustained change in a definite direction.

The changes in the earth's crust that have occupied the periods between the six great " revolutions " of geological time may not have been, probably were not, mere " pendulations " towards a state of equilibrium. They may have had a course defined by the major oscillations of the earth's crust, so that, *e.g.*, during a period of progressive elevation movements of subsidence were more than compensated by the upward movement. For a discussion on the inter-revolutionary disturbances of the earth's crust, see Joly (1925, Appendix to ch. viii., p. 144). The latter states that " in the ages following a great revolution this explanation [the attribution of mountain-formation to volume changes in the substratum underlying the earth's crust] involves no more than a recognition of the fact that in the region just below the surface-crust of the earth *slow movements arising from final consolidation* probably continue for long periods ". He recognises, however, that subordinate cataclysmic events may take place in the substratum owing to local instability of the latter.

I ought finally to point out that very often the destruction of individuals arising either from over-population or from catastrophic events, will often be quite indiscriminate and have no selective effect (cf. Rabaud, *l.c.*, p. 353).

Observations on the Action of a Selective Death-rate in Nature

There are eighteen series of observations known to me in which the effect of a death-rate has been studied with a view to ascertaining if the latter is selective. The details of these observations are presented with the various criticisms which have been made. The majority of these observations have been criticised by Pearl (1917) ; but I have deemed it advisable to offer here the result of a fresh examination of these data with some observations not included in Pearl's survey.

Of the eighteen series in question one only (Weldon, 1897, 1898) consists of observations made on more than one generation, so that we cannot readily form an opinion as to the effects of such selection in producing continuous change. Even Weldon's study on selection in *Carcinus maenas* did not consist of more than three series of observations made in 1893, 1895 and 1898. The observations did in fact reveal a progressive change over the period in question, and control observations were made. The latter are ambiguous ; but at least they show that the control animals did not manifest the change observed in those exposed to the selective conditions. Moreover, the experimental subjection of crabs to conditions similar to those deemed to be selective in nature resulted in a selective death-rate which altered the character of the experimental group of animals in the same way as the natural conditions were held to modify it. Biometrical objections have been lodged against Weldon's claim that selection is demonstrable (Vernon, 1903); and there is no proof that the change produced is hereditary. The amount of change observed was very slight. Thus, in crabs 14·5 mm. long the carapace width fell from 76·26 per cent in 1893 to 74·44 per cent in 1898. It is quite possible that the alterations of proportion witnessed were produced by the direct effect of the changed conditions. It seems to me that this ambiguity militates somewhat against the proof of any permanent selective change, and along with Vernon's objections suggests that we cannot take the actual results at their face value. The characters of the controls, however, and the experiments mentioned above, go some way towards showing that a selective death-rate was operative in the generation kept under such observation.

Positive selection of this order, which was operative on a single generation, is recorded by Crampton (1904), Harris (1910 and 1912), and possibly by Lutz (1915). Poulton and Saunders (1898) and di Cesnola (1909) showed that a certain type may be eliminated, if kept on a non-harmonious background. These experiments are important as showing that certain types, if rendered conspicuous by their surroundings, are destroyed. But the utility of the colours and pattern in question could only be selective, if at the same time it could be proved that they were accompanied by the habit of choosing the appropriate background.

Crampton's observations on the larvæ of *Philosamia* are important; but, even if we overlook his own criticisms as to the unsatisfactory method of measurement which he adopted, on the ground that the latter would introduce error in measuring survivors and eliminated and could therefore be evaluated, they do not establish the value of the actual character modified by selective elimination, which, as Crampton points out, is not one of use in the larval state. It is possible, however, as Crampton points out, that this character was influenced by correlation with some physiological character on which the death or survival of the larvæ depended. The results obtained by Bumpus (1898) are regarded as biometrically unsatisfactory by Harris (1911), and in any case the cause of death does not seem definitely established in this case. An alternative explanation, viz. intercolonial variation, is likely to account for the differences observed in Boycott's study of *Cepea nemoralis* (1913). The numbers of observations made by Jameson (1898), Davenport (1908), and Harrison (1920 A) are inadequate. No evidence of selection was obtained by di Cesnola [1] (1907), Weldon [1] (1901), Kellog and Bell (1904), Pearl (1911), and Haviland and Pitt (1916). Experimental study of the utility of slight structural differences is comparatively rare. In addition to the studies of di Cesnola, and Poulton and Saunders (p. 236), allusion may be made to Swynnerton's experiments on the survival value of slight differences in the power of flight in Lepidoptera (1926, p. 495). This author concluded that reduced power of flight produced by slight artificial mutilation of the wings did not operate unfavourably against the mutilated animals. Reighard (1908) found that when members of twenty-one species of conspicuously coloured coral-reef fishes were fed to the Grey Snapper (*Lutianus*), they were all with one ambiguous exception taken by the latter. Reighard concludes that the coloration of these fish is without biological significance as far as "protective conspicuousness" is concerned. The Grey Snapper is apparently the most common carnivore among the reefs of the area in which the observations were carried out (the Tortugas). Reighard does not say if he considered examination of the other carnivorous fish superfluous.

With the exception of Weldon's results, these studies can only be treated as evidence bearing upon the incidence

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[1] Both these authors found some evidence of "periodic" selection.

of a death-rate on a single generation. As such there is enough in them to show that the death-rate is sometimes selective, or, as Pearl puts it, the survivors differ from the eliminated. They show that at least one condition of Natural Selection is fulfilled. Unfortunately they do not tell us to what extent modification of the hereditary constitution of a stock takes place under these conditions. In selection of this order, until we know that the genotypic basis is definitely altered, we cannot accept it at the current valuation. Nevertheless, unless we wish to doubt the validity of those observations and experiments in which the death-rate was seen to be selective, we must admit that there is selection of slight differences. If any of these are genotypic, and if fresh variants arise of a genotypic nature that are of still greater value, it is likely that they will be preserved and the stock will undergo progressive modification.

In his *Mendel's Principles of Heredity*, Bateson laid it down that " there is nothing in Mendelian discovery which runs counter to the cardinal doctrine that species have arisen by means of Natural Selection . . . By the arbitrament of Natural Selection all must succeed or fail. Nevertheless, the result of modern inquiry has been to deprive that principle of those supernatural attributes with which it has sometimes been invested "; and again, "the conception of evolution as proceeding through the gradual transformation of masses of individuals by the accumulation of impalpable changes is one that the study of genetics shows immediately to be false ". The distinction between "definite, integral change" and " the accumulation of impalpable changes " erected by Bateson seems to us to-day less important than was originally supposed. The revelation of the extremely complex factorial basis of many characters renders it very likely that the phenotypic expression of such characters will be permanently modified by very slight factorial changes, in other words, that strictly genotypic change may have slight phenotypic expression. If such change is of survival value, then the picture of selection and its materials drawn by Darwin does not differ essentially from that drawn by the geneticist.

It may of course be believed by the latter that in some cases a character may undergo definite integral change, and that the organism bearing such a character may multiply without the aid of selection (see p. 219). When a character is proved to be of survival value, the antithesis between Natural Selection and the results of genetic study seems to be unimportant. The real disability with regard to Natural Selection is the difficulty of proving the survival value of a multitude of small differences between species. I do not think that there can be any doubt that some trivial differences are of value, and that inferentially we may regard it as extremely likely that they are preserved and accumulated by Natural Selection. But we labour under the necessity of explaining the use of a multiplicity of differences that at present defy our ingenuity.

At this point it will be convenient to comment briefly on Darwin's theory of Sexual Selection. The effects of the latter, as its author was careful to point out (1871, p. 324), are sometimes impossible to distinguish from Natural Selection, for example in the development of differentiated sensory and prehensile organs in the two sexes. When, however, it is a question of ornamentation, scent-glands and organs of attack, wherein the males and females differ, the effect of sexual selection may be readily studied. It should be noted that differences of this order are most marked in highly organised animals such as certain Arthropoda and the Vertebrata, and that their incidence seems to be somewhat capricious. For example, Darwin (*l.c.*, p. 337) pointed out that the sexes rarely differ in this respect in the Rodentia. Even within a single genus of Birds the sexes of one species may be clearly distinguished (*Parus cristatus*), or more or less indistinguishable (*Parus palustris*). With regard to organs, superiority in the size or efficiency of which might give one male an advantage over a rival, there need not be much doubt that *on the whole* advantage of this sort might lead to a selective result, though the latter must depend very largely on the extent to which unsuccessful males can eventually succeed in finding a mate. When we attempt, however, to explain. the origin of differences in organs of attraction or ornamentation by sexual selection, difficulties arise. The distinctions in question presuppose differences in taste on the part of the female, the origin of which must be accounted for. There is considerable doubt as to whether differences in ornament, display or antics during courtship are of weight in the actual selection of a partner, and, if they only acquire an important status as a stimulant after the partner has been selected, whether differences of this sort are likely to determine whether coitus is acceptable or the reverse. The apparently capricious development of sexual dimorphism mentioned above must make us a little sceptical on this subject.

It is well known that the secondary sexual characters are intimately dependent for their expression on the glandular secretions of the reproductive system. Whether the qualitative and quantitative differences in the sex-hormones that determine interspecific character-differences are established by selection or by a physiological orthogenesis, or whether we should recognise with Cunningham (1920 and bibliography) that the secondary sexual characters are produced by regularly recurrent stimuli made heritable "in association with the physiological conditions in which they were originally produced", is *sub judice* at the present time.

The conclusion that we may allow ourselves to form as to the likelihood that Natural Selection is a means whereby new characters are spread in a population is as follows: (1) Selective elimination may be of such a nature that the survivors are distinguished from the eliminated by relatively slight differences which, theoretically at least, may have a genotypic basis, though we have no exact evidence from selection on a population in nature as to the amount of heritable variation that is actually selected. (2) The differences between species are only occasionally shown to be sufficiently correlated with appropriate differences in habit to be accepted on strict analysis as adaptive. (3) The chain of evidence that indicates the adaptive origin of mimicry in Lepidoptera is perhaps the most complete and satisfactory. It is far more substantial than that which has been produced in favour of other explanations of this phenomenon. The data are, however, in need of systematic presentation, and in addition there are still some criticisms to be dealt with. (4) The demonstration of adaptive differences between allied species and the more plentiful evidence of such differences between genera does not involve us in the admission that such differences must necessarily have arisen by Natural Selection. (5) There remains a very large residuum of differences between allied species and races which, by reason of their position or rôle in the life of the organism, are not likely to be adaptive. It cannot be proved that they are non-adaptive ; but the burden of proof rests on the doctrine of Natural Selection. A certain proportion of interspecific and interracial differences proposed in systematic literature may be disregarded from this point of view, as they are probably produced by plastic response to environmental stimuli. (6) There is no satisfactory evidence at present available of the modification of a structure through its being correlated with one transformed by selection. The prevalence of correlation of one sort or another (see Chapter VII.) renders it likely that such change may occur ; but it is not likely to occur when specifically differentiated parts have no common organogenetic basis, mechanical relation or physiological dependence. (7) However sceptical we may be as to the selective advantage of slight interspecific and interracial differences, it must nevertheless be borne in mind that Natural Selection provides a logical explanation of the spread of a new character in a population.

I think we ought to conclude that there is some circumstantial evidence that new characters may attain a high numerical frequency in a population, either through the transformation of a large number of individuals by environmental stimulus, or through the operation of Natural

Selection. The proof that such transformation has taken place regularly by these means is not very strong, and does not allow us to speak authoritatively as to the method by which variants have increased numerically as a general rule. It may subsequently be shown, as the result of more intensive study, that one or the other of these agencies of transformation is more potent than I have allowed, or that together they constitute an effective explanation of the numerical increase of variants. The lack of convincing evidence that induced modifications are regularly and frequently inherited, and the suspicion that many interspecific and intervarietal differences are devoid of survival value, compel us to consider whether new variants of purely germinal origin may not spread in a population through normal multiplication without any adventitious aid from Natural Selection.

(3) The Multiplication of Individuals bearing non-advantageous Characters

Such variants might attain a high numerical frequency either if they arose in a few individuals and the multiplication of the latter were unrestricted, or if the " mutant " character arose from the parent stock on many occasions and in many places. The second suggestion is not supported by much evidence. When a novel form has appeared sporadically under human observation in nature (*e.g.* the *lacticolor* form of *Abraxas grossulariata*), such appearances are not to be taken as representing the original acts of " mutation " ; for as Morgan points out (1919, p. 248), " when these (the mutant characters) are recessive it is probable in most cases that the actual mutation occurred several generations before the mutated genes came together to produce the mutant character ". When mutant types have occurred under control conditions which exclude the possibility of their having been induced by environmental influences, the same type of mutant only occurs very infrequently. In *Drosophila* " vermilion " (*e.g.*) has occurred six times. The only variant form in *Drosophila* that has occurred with any frequency, viz. " notch ", is not regarded by Morgan (*l.c.*, p. 249) as of " mutational " status. The " red-eye " mutant of *Gammarus chevreuxii* (Sexton and Wing (1916); Sexton and Allen (1920)) made its appearance first in only a very few individuals. Gates (1921) records several instances of the recurrent appearance of the same mutants in plants. None of these, however, lend support to the view that a mutant character may arise separately in a large number of individuals.

I do not say that the multiple origin of mutants should be excluded from consideration ; but I do not think there is much evidence for it. As far as observation is concerned, all we know is that so-called mutant races occur in nature, without knowing precisely how they have become established. We must look, therefore, to a few variant individuals for the origin of a mutant race. How, then, can we explain the survival and increase in numbers of such individuals, if the new character is not advantageous ?

At first sight this does not seem to be a very difficult question to answer. It may be held that the individuals in which a new character appears, provided that there are enough to give rise to a second generation, will simply increase and disperse themselves by normal multiplication. This sort of increase, however, is obviously dependent on the survival of enough of the new variants to give rise to a second generation, and on this subject we are seriously in need of enlightenment. In a population with a fairly balanced birth- and death-rate the chances favouring the survival of a few mutants are slight unless they have some advantage in the struggle for existence. The difficulty may be briefly expressed in the question: Are there usually sources of food and opportunities for successful reproduction and growth available for uncommon variants ? The answer is : We do not know. In view of the very considerable amount of destruction that goes on, either from the direct effect of adverse climatic and other conditions, or from competition for limited sources of food, etc., we ought to be very sceptical as to the chances of survival enjoyed by single variant individuals. As we have already seen, there is a possibility that a new variant may arise in a part of an area in which a change to some other mode of life may be facilitated by there being access to some untenanted habitat. Thus in a terrestrial species a new mutant might find it possible to enter an arboreal habitat. We must, however, be prepared to account for a change in habit besides that of structure, if the new form avails itself of this opportunity, and, as I have already pointed out, this involves a large amount of coincidence.

Among the species of Mollusca with which I am familiar, several species of a more or less fixed habit occasionally make themselves at home in places not usually favoured. Thus *Helix aspersa* will occasionally colonise trees, and *Cepea nemoralis* may be found plentifully in some sand-dune areas. In West Cornwall and the Scilly Isles, Mr. O. W. Richards and myself found the characteristic dune-snail, *Cochlicella barbara*, on walls and in hedges, and conversely, several species of *Hyalinia* were found on dunes, though the bulk of our examples were taken from walls and similar habitats. A more remarkable change of habitat is recorded by Thienemann (1924, p. 53), who states that in certain parts of Germany the characteristically terrestrial snail, *Lauria cylindracea*, is to be found living in streams.

The extent to which in any area already inhabited by a species there is room available for new forms, seems to me to be very uncertain. Much valuable information might be obtained if field collectors and ecologists would seriously study this question. Elton (1924) has shown that one process at least may provide for this. From a study of the periodic fluctuations in numbers in various mammals, he has shown that a periodic reduction in numbers takes place as the result of epidemics, bad weather and similar catastrophes. Among these forms there is a time when the numbers of a species are at their lowest and competition is reduced, and there is room in a given habitat for more individuals than it can normally sustain. At such times a new and uncommon variant will have a chance of surviving and increasing numerically.

Elton does not, however, discuss an important issue raised by this suggestion. New variants are more likely to occur during periods when the population is numerous, and I think that it is likewise true that, all things being equal, during a period when the population is at a minimum, there is a likelihood that new variants will be rare. Broadly looked at, the suggestion confronts us with a dilemma, for the period when new mutants are likely to be most numerous is that in which their survival and multiplication are least likely.

However, in making suggestions as to the sort of opportunities that there may be for individuals of a novel type to spread and multiply, we must not lose sight of the fact that the chances must be very favourable that bring about the appearance of a mutant in the right sort of area to insure its survival.

Any theory that seeks to explain the origin and multiplication of new variants on the assumption that they are purely germinal in origin, and that they can increase without some adventitious assistance, raises almost as many difficulties as it eludes. Our data as to the changes that take place in the constitution of natural populations are so scanty that we are deprived of any means of ascertaining whether in nature opportunities are available for the survival and numerical increase of such variants. This objection seems to be so serious when taken in conjunction with the mathematical investigations into the chances of the survival of a mutation that confers no advantage on its possessor (Fisher, 1922), that many students of these problems are apparently inclined to regard some measure of selection as necessary for the spread of new characters in a population.

CHAPTER VII

CORRELATION AND THE ORIGIN OF GROUPS

In the preceding chapter we dealt with the origin of variation and the means by which a new variant increases numerically. Although we discussed the part played by all-round adaptation in determining survival, we did not consider the origin of the groups conventionally treated as species, which are usually distinguished one from another by several individual characters.

As we saw in Chapter I., the process of evolution does not entail the production of standardised groups or units. The groups which we recognise as species and varieties differ from each other in manifold ways, the number of differentiated characters and the degree of divergence between the individual characters being very varied. I have in several places stressed the fact that one of the means by which we can recognise groups in the world of organic beings is by the presence of some measure of correlation between differentiated characters, and before proceeding to discuss the origin of such groups, I ought to say something about the amount of correlation that exists between the characters of species and in the natural populations from which they have been abstracted.

I stated in Chapter II. that not only are systematic species very diverse in their constitution, but also, being very often founded on a few samples from different localities, we cannot state to what extent the larger assemblages from which they are taken actually reproduce the association of characters and the discontinuity seen in such local samples. We very often, it is true, obtain from widely separated areas, individuals which are similar in very many respects. On the other hand, we cannot avoid the conclusion that natural populations are very often so diversified as to prevent us from regarding them as homogeneous in the systematic sense. As the relation of systematic species to natural populations is so imperfectly known we ought, in attempting to probe the causes of evolutionary divergence, to think not so much in terms of species as of the actual degree of correlation between characters that we know to occur in specific cases. Sometimes we find small local assemblages in which several characters are highly correlated ; sometimes such correlation is extended over a wider array of individuals. On the other hand, both local groups and larger populations may sometimes be composed of loosely correlated elements. The explanations we may be able to offer of the origin of such groups must vary according to whether we are dealing with high or low correlation of the variates. If one or all of the more widely accepted theories of evolution is beset with difficulties in one set of circumstances, it by no means follows that it does not provide a satisfactory solution in others. I have laid special stress in this chapter on high correlation and homogeneousness because the current theories seem to encounter special difficulty in dealing with this phenomenon. At the same time I do not wish to suggest that natural populations may not sometimes have a constitution quite explicable in terms of one or another of these theories. I feel, however, that stress must be placed on high correlation because of the quite noticeable tendency for characters to " hang together ", and for groups, whether of the status of systematic species or of races, to be recognisable by this tendency. Even in very polymorphic species we find some, if not all, of the distinctive characters correlated. Thus in the plastic and variable species of Limpet, *Patella athletica* and *vulgata*, I have found in samples from many parts of the N.W. European littoral a steady association ($r = \cdot 5$) of certain characters. The same is true of the lip-colour, and the form of dart and shell in the Wood and Garden Snails, and as far as I can at present ascertain in the surface-sculpture, web-proportions and the ratio of the arms in the common *Octopus vulgaris*, by which characters the latter is systematically distinguished from its near allies. Weldon (1893) and Warren (1897) found that various characters of local races of species of Decapod Crustacea have approximately the same correlation coefficients. I think, therefore, that with due consideration to the causes that may lead to less marked association, we must be prepared to pay special attention to the occurrence of high correlation.

The question as to whether there is, as I believe there to be, a close relationship between the correlation of specific characters and the discontinuity or continuity between species may seem a formal one. As, however, it is usually the custom to speak of the " gaps " or the continuity, as the case may be, between species without defining the nature of such gaps or such continuity, I must attempt to indicate the relationship in question.

When we take up the study of any species that have been at all intensively studied we find, as I have already said, that they may be completely discontinuous in all the characters that have been examined, or that some characters are discontinuous and others are not, or finally that complete continuity in all the characters may occur. I need hardly say that the terms "continuity" and "discontinuity" are relative, and dependent upon an arbitrary measure of the amount of difference. As we have already seen, the only measure of discontinuity that is not wholly arbitrary is that provided by a single meristic unit. Otherwise our notions of discontinuity are dependent on nothing more precise than the recognition of some kind of hiatus in a series of variates.

Further consideration of such species may show us that, although a given series of forms is continuous, many more individuals of a given constitution may be found at certain stages in the series than at others. It is this that enables us to recognise species and races in spite of the presence of intermediates. Such species, whether we regard them as " incipient " or as linked up by more or less heterozygous individuals, are recognised by the correlation of several characters, and the characters of the intermediates may exhibit a condition midway between the conditions exhibited by the individuals of more highly correlated groups. But they may also exhibit another kind of intermediacy, and represent combinations of characters found in the groups of more frequently associated correlates.

Broadly speaking, then, we have to deal with two kinds of relationship between species—namely, discontinuous and continuous, and we should try to gauge the relation of the one to the other. Are two groups which are continuously related actually terms in a series, in which various characters are becoming more highly correlated through, *e.g.*, progressive selection of those two types, or are they groups fundamentally discontinuous between which a fortuitous population of intermediates is established through, *e.g.*, the influence of the environment or the interactions of genetic factors brought together by crossing ? Each case must be settled on its merits, and I have no doubt that intermediacy may be due to both causes. But often it will be very difficult to see any real distinction between these alternatives. The attempts made to write off all intermediates as fortuitous and due to either the effect of the environment or to various expressions of heterozygousness (cf. Bateson, 1909, p. 235 and following) does not seem to me to establish the essential discontinuity of species, if it is not at the same time shown that a permanent population intermediate between groups with more highly correlated characters cannot be maintained. It seems likely, then, that continuously related species may be either partly divergent or groups reintegrated by crossing, and that the former represent preliminary stages of the more considerable divergences seen in discontinuous species.

Since the characters of many naturally divergent groups are interchangeable and intermediates representing recombinations are often to be found, it follows that in such cases correlation will not be as marked as when species are discontinuously related in all the characters studied, in which case correlation of the latter will be high. High correlation and discontinuity seem, then, to be closely related, and to be different expressions of the same phenomenon, at least as far as the characters of divergent groups are concerned. When Pearson (1901, p. 326) states that if " correlation is imperfect [? *sc.* low] . . . statistical theory shows us discontinuity ", I think I am right in assuming from the context that he refers to parent-offspring correlation in respect of one character.

In discussions involving the question of the divergence of species it is, as I have said, customary to discuss the latter in terms of the " gaps " or of the continuity between them. In this chapter I wish to emphasise the relation between the individual characters by which species are distinguished, by dealing exclusively with the correlation of the latter.

We might explain such correlation by assuming that, if each new character may be induced by some environmental change, all the individuals bearing the characters distinguishing any given species or race may have been simultaneously exposed to several modifying influences of this nature, or to a single change which affected several characters at the same time. Or we may assume that these individuals are subjected to coincidental processes of selection in respect to the characters, or to a single crisis of selection which affected several characters correlatively Finally, we might believe that germinal change in several characters may occur simultaneously in several individuals, which may multiply and spread according to the availability of unoccupied areas or habitats, rather than in virtue of any advantage such change may confer on the organisms exhibiting it. On each of these hypotheses the association of characters is fortuitous, and the individual characters have no other relationship one with another save that of coincidence. But when there is shown to be a more intimate association between them, their correlation may be of an obligatory nature. If we are satisfied that such an affinity exists in some instances, it does not follow that the basis of association provided by one or the other of the orthodox evolutionary hypotheses is without importance. All that it is necessary to anticipate at this stage of our argument is that, if we are sceptical as to the efficacy of these hypotheses to explain certain kinds of correlation, there may be an alternative explanation of the latter.

It will be most convenient for our purpose first to examine the various types of correlation, paying special attention to those in which the association is obligatory, and then to take up the question whether the formation of species can be satisfactorily explained by the current theories of evolution, or whether we must invoke any supplementary explanations of the association of the characters of species.

ON CORRELATION IN GENERAL

The term " correlation " is used to describe several phenomena which are not of the same nature. Thus homologous parts and right and left members of metamerically disposed parts tend to vary together (Darwin). Again, the occurrence of certain secondary sexual characters are said to be correlated with the presence of the ovary or testis. In these two instances the coincidence of variation in the two correlated parts is of a different order, and is due to different causes. In the first case, the capacity for variation is held to be more or less identical because the homologous structures are developed from identical material. In the second case, one component of a correlated pair stands to the other as cause to effect. Darwin (1875, ch. xxv.) devoted much time to the study of correlation ; but he was more concerned with the collection of data than with an inquiry into the causes of such association.

Dürken (1921) has distinguished the three following phenomena, which are usually classed together, as Correlation :

(1) *Relation.*—The unilateral dependence of a structure on an internal or external factor on which the structure itself has no effect (*e.g.* the relation of the optic capsule to the embryonic lens in Vertebrata).

(2) *Correlation.*—The reciprocal dependence of two associated parts (of such a nature that alteration of one leads

to the alteration of the other); *e.g.* the reciprocal dependence of the extremities and the nervous system during development. (1) and (2) include all causal associations.

(3) *Combination.*—The "static" coincidence of similar variables, without any reciprocal or unilateral dependence. "Combined relation" is used to designate the dependence of several parts on a single stimulus; *e.g.* specialisation of several organs for the same function; individual dependence of several organs upon sex hormones or on an external stimulus (cf. Sumner, 1915).

Graham Kerr (1926) has distinguished between *primary* or *gametic* and *secondary* or *physiological* correlation. The first includes, for example, the association of characters through linkage; the second implies such a relation as that between the state of activity of an endocrine organ and the structures or processes affected by it. This subdivision seems to me a very convenient and natural one, and we will use it in the course of this review. Kerr's "primary or genetic correlation" seems to me more suitable than Plate's "idioplasmatische oder determinative Korrelation" (1913, p. 132).

(1) Gametic Correlation

Let us suppose that two forms to which specific rank is given differ in respect of five well-marked characters, and have the constitution A B C D E and A′ B′ C′ D′ E′. Do those characters behave in heredity as though they each formed part of an organic whole so that they are each affected in some measure by the common environment and the common basis in which they are implanted? Does, indeed, the behaviour of these characters suggest that such a common environment or basis exists at all?

The most that we are justified in expecting is information as to whether characters which are recognised as collectively distinguishing species come out of a cross in the same state of association as they went in, and whether they are all dominant or all recessive.

When species are successfully crossed so as to yield fertile offspring, the factors for the various contrasted characters most frequently tend to behave in complete independence. The complex of specific characters is dissociated and made subject to the ordinary laws of random assortment. The reappearance of the grand-parental character-complex in species-crosses is therefore in a general way determined by the segregation and random assortment of as many factors as may be involved. Thus Lotsy (in Babcock and Clausen, p. 222), in his F_3 populations of *Antirrhinum majus* × *A. molle*, obtained one pure *A. molle* segregate in 209 plants, while Harrison (1917), in his cross of *Poecilopsis pomonaria* and *isabellae*, obtained one pure *isabellae* and one almost pure *pomonaria* segregate in fifteen males.

On the other hand, there is a good deal of evidence that groups of characters may behave on crossing as co-ordinated systems that are not thus dissociated. I think it will be plain from the evidence submitted that this co-ordination may have more than one cause.

A. Inasmuch as a relation between linkage and correlation has on several occasions (Collins, 1912; Babcock and Clausen, 1918; Robson, 1923) been suggested, and as the association of specific characters may be regarded as affected by correlation, it is necessary to consider these phenomena.

I should point out that linkage does not necessarily produce correlation of visible characters. Two genes may be located in the same chromosome; but if one is dominant and the other recessive there will be no high frequency of association in the resulting phenotypes. Linkage, therefore, does not necessarily involve somatic correlation, though correlation may be due to linkage. I am indebted to Captain C. Diver for pointing this fact out to me.

At first sight there would seem to be very little relation between linkage as it has been studied in the *Drosophila* mutants and the association of specific characters. The chances of linkage depend on the number of chromosomes. If the latter is small, the chances are high; if it is large, the chances are low. On the whole, then, it would follow that species with a large number of chromosomes would exhibit few stable character-associations, if coincidence in the same chromosome were the only mechanism of association. The basis of association is not the morphological species, but the chromosome; thus within the species *Drosophila melanogaster* we have four groups of linked genes which correspond to the number of chromosomes. Be that as it may, we have not much evidence that the characters of taxonomic species behave as though they were linked. Surface (1916) has shown that in his *Avena fatua* × *sativa* crosses there is an association of the characters distinguishing the wild species from *sativa*. But it is as yet uncertain if such association is actually of the same order as that found in *Drosophila*.

From the foregoing remarks it will be seen that it would be very difficult to associate linkage with such a process of correlation as is present in the character combinations of species. Linkage phenomena provide a clue to certain types of somatic correlation; and it may possibly be shown that a part of the correlation seen between the characters of some species may rest on this basis. It may be pointed out that, just as the cross-over values vary in different cases in *Drosophila*, so the coefficient of correlation varies very much in the associated characters of species.

B. In addition to the linkage observed in *Drosophila*, for which a special mechanism for the association of characters is currently accepted, there are several instances of association for which either linkage of the *Drosophila* type has been suggested or a factorial basis of association suggested. These are represented by Bateson's original case in Sweet Peas (Bateson, 1909, p. 148), and the results of Vilmorin and Bateson (*Pisum*, 1911), Surface (*Avena*, 1916), Castle and Wright (Rats, 1916), Philipps (Birds, 1921) and a few others.

C. Other instances of association for which no explanation is provided are fairly plentiful. Engledow (1920) states that glume and grain-length in Wheat are genetic inseparables, " remaining associated throughout the vicissitudes attendant on the production of F_2 and F_3 plants ". Harrison (1916*a*,

p. 145), in crosses of *Lycia hirtaria* and *Poecilopsis pomonaria* and of the latter and *P. isabellae*, found what he called "segregation *en bloc*" of certain specific characters. In these cases the available number of F_2 individuals is not very high. Kristofferson (1922, p. 44), in his *Malva* crosses, found the distinguishing characters of *oxyloba* and *parviflora* segregate together, the *oxyloba* and *parviflora* types occurring in the F_2 generation in a very close approximation in a 3 : 1 ratio. Philipps (1915) reports correlation of a not very high order between parental characters in the F_2 offspring of a cross between the Mallard and Pintail duck. We may include here certain obscure cases, the genetic interpretation of which I am not competent to discuss, in which the characters of mutant types keep together *en bloc* (*Oenothera*-mutants, Gates, 1915 ; *Zea*- "mutants", Collins, 1917).

D. We sometimes find that the characters of one parent in a species-cross are either regained on a single back cross or substantially modified in the direction of the parent. These are to be found in *Oporabia* (Harrison, 1920), in Ducks (Phillips, 1915), in Wheat and Rye crosses (Jesenko, 1913), and in *Cochlearia* (Crane and Gairdner, 1923). This recovery of uniparental type on back crossing is rare. Harrison (*l.c.*) and Phillips (*l.c.*) have advanced alternative theories to account for such reversionary back crosses.

It should be noted that "dominance *en bloc*" is reported in *Nicotiana tabacum* and *sylvestris* crosses (Goodspeed and Clausen, 1917, p. 321), and by Harrison (1917, p. 281) in *Poecilopsis*. To explain this phenomenon in *Nicotiana*, the first-named authors advanced their theory of the "reaction system", according to which they visualise the total set of factors of a species as harmoniously integrated.

E. Apart from the phenomena described in the preceding sections which may possibly account for part of the correlation observed between specific characters, there is a further means of association which may be classed under gametic correlation. The offspring born from two parents homozygous for the same set of characters will show those characters in complete association. In nature it may occasionally happen that such " pure-bred " parents or their offspring are accidentally isolated so as to yield a pure-bred colony in which a number of characters are highly correlated. The homogeneousness of an isolated population is largely dependent on (*a*) the degree of homozygousness for all the characters borne by the individuals isolated in the first instance, and (*b*) the completeness of isolation. If, however, we wish to explain by this means the uniformity of a species differing from allied species in several non-adaptive characters not present in the latter, we would have to assume that such characters appeared simultaneously in enough individuals of both sexes to secure the matings necessary to found a homozygous stock.

(2) Physiological Correlation

The relationship between a secondary sexual character and the primary sexual organs, or between two structures which are dependent on each other in development, involves a causal correlation. Furthermore, two or more characters may be equally dependent on a single stimulus (*Combined Relation*, Dürken). For example, Herbst (1897) found that the development of the skeleton and of the gut in *Sphaerechinus* are both dependent on the presence of SO_4 in the medium. In plants receiving an insufficiency of light lengthening of the internodes, loss of chlorophyll and reduction in the size of leaves are commonly associated. Whether any of the more normal differences that jointly distinguish species and varieties are of this nature, is very uncertain, but it is possible. It may be that many of the differentia relating to size and proportion of parts are due to the reciprocal relation of the latter during growth.

When we have genetic or other evidence to show that an association is due to linkage or to homozygousness, it is possible to assign a cause to correlation, or if we know that there is an actual dependence that can be experimentally demonstrated. But when such evidence is not forthcoming, it is in practice impossible to decide the basis of correlation. It is sometimes possible to decide whether a given case of correlation is due to genetic or physiological causes by a process of evaluation. Thus it is likely that the long-headedness and tall stature of the Nordic race of European man are not dependent on a physiological (*i.e.* causal) relationship, for long-headedness is found associated with short stature in the Mediterranean race.

Apart from experiment the only other means we have of deciding as to the basis of correlation is the rather dubious indication provided by the frequency of association. A causal or physiological association is bound *on the whole* to yield a high correlation. Gametic association, on the other hand, need not be productive of high correlation.

I do not think we need hesitate to believe that structural characters are sometimes correlated with physiological ones. This fact has long been known and utilised by breeders and fanciers, and striking examples are given by Darwin (1859, 1875), by Harris, Blakeslee and Warner (1917), for egg-production and pigmentation of the ear-lobe in fowls, and by Harris (1916) for certain characters in plants.

The correlation of parts is often discussed on the assumption that structures developed from the same germ-layer, or from the same area, tend to exhibit similar variation. The phenomena of development also seem to indicate some measure of organogenetic correlation (see discussion in Jenkinson (1909, p. 271)). But I do not think that we can as yet decide whether, for example, the observed correlation between the length and breadth indices of a Lamellibranch shell is gametic or physiological. It is certainly not true that parts derived from the same germ-layer, or belonging to the same area, are equally correlated. Thus Warren (1897) found that the shape of various portions of the carapace of *Carcinus menas* are correlated in very various degrees, some being as frequently associated as $r = \cdot 76$, others as low as $r = \cdot 08$ and $\cdot 23$.

Having thus reviewed the causes of correlation, let us now return to the question whether the coincidental occurrence of characters assumed to be produced in the same members of a population either by Natural Selection, or by the effects of the environment or by Mutation, can adequately explain the association of specific characters.

(1) If we admit the possibility that heritable variation may be induced in the germ-cells, we must consider the origin of a species or of some definitely characterised section of a population as likely to take place in two possible ways. We may believe that, when it produces a heritable change, the stimulus of the environment is (*a*) dependent on the appropriate occurrence of complementary change in the germinal material or the physiological constitution of the individuals exposed to such stimuli, or (*b*) operative by itself and without any complementary change. When we are dealing with a very polymorphic population or a species characterised by intense local diversification with low correlation of all the characters, there is no special difficulty in accounting for its constitution on the assumption that its hereditary characters are environmental in origin. Our only difficulty is the preliminary one of proving the latter, and of showing that the environment is sufficiently diversified to give rise to the local differences in the population. When, however, there is a substantial measure of correlation between the characters, special difficulties arise. On the first assumption ((*a*) above) we must be prepared to justify the belief that the germinal changes, or other individual differences complementary to the environmental stimuli, take place in a large number of individuals and coincide with the appropriate stimuli that evoke the various characters. This involves a very confident reliance on coincidence, if each differentiated character is considered to be dependent on a separate stimulus. It is quite likely, however, that a single environmental stimulus may have effect upon several characters, and in one instance at least I think we may regard this as proved so far as correlation in one generation is concerned (Sumner, 1915). Many instances could be given of diverse somatic changes induced in the same population apparently by single environmental factors. But

in these we lack objective evidence that such change is hereditary.

If, however, the change in the individual organisms which we regard as complementary to the environmental stimuli is not of the nature of a mutational germinal change, but is thought of as some physiological crisis in the development of the adult individuals exposed to the environmental change, it is easier to see how mass-transformation might take place ; for it is likely that most of these individuals would sooner or later pass through the postulated developmental crisis.

The extent to which several characters might be influenced correlatively by reaction of a single part to an environmental stimulus is very obscure. The reader is referred to the discussion on correlation (p. 228 and following). I believe that, when the dependence of one part on another is of a *causal* nature, the modification of the one by environmental change might very well lead to a corresponding alteration of the other. The subject is, however, largely speculative at present, and we possess little evidence as to the actual operation of this principle.

(*b*) If the factors of the environment are regarded as capable of producing the various characters of a population without any complementary change in the germinal material or in any special physiological activity of the organisms exposed to such change, it is not so difficult to imagine how mass-transformation involving several characters might be effective. We have reason to believe (Chapter VI.) that change of this order is a less likely event than that considered in (*a*), though it is by no means to be excluded as a possibility. But on this assumption, as well as on that previously dealt with, when we try to account for a condition approaching homogeneousness of character-association maintained after the individuals bearing such associated characters spread beyond the area in which they received the new characters (*v.* p. 174), we must rely on all the characters remaining singularly stable and insusceptible to new conditions. In other words we find the difficulty outlined on p. 174 increased, because there are more characters involved. It is true that natural populations are not by any means homogeneous. Their diversity of composition has been already admitted. But, if we conclude, as I think we must, that after receiving environmental modification animals and plants may multiply and extend their range beyond the scene of their transformation, even the relative homogeneousness of natural populations with which we are familiar could only be maintained by a very singular degree of insusceptibility to the environment on the part of each character. In the case of markedly homogeneous species the difficulty of explaining the constancy of all the correlated characters becomes, on the hypothesis under discussion, a very grave one.

(2) If variation is held to be purely germinal in origin and the multiplication of variants is deemed to take place through Natural Selection, the correlation of several characters in a population may arise as the result of as many separate selective crises, or because the population is subject to selection in respect to a character with which other characters have some intimate basis of correlation. In the first case each differentiated character is produced by selection ; in the second it is sufficient for one character only to be thus modified. Pearson (1903, p. 2), in discussing the mathematical aspect of correlation, expressed the opinion that Natural Selection is probably the chief factor in causing correlation. Darwin himself, not believing that all the differentia of species can be regarded as adaptive in origin, invoked correlation as an additional means of answering Bronn's scepticism as to how many parts of the organisation could have been modified at the same time through selection. In this he has been followed by most modern exponents of this doctrine.

I do not think we need trouble to discuss whether each character by which a species differs from its allies is an individual product of Natural Selection. The general case for selection has been already discussed. We may readily believe that the various separate features of which the wing-pattern of a mimetic butterfly (p. 190) is made up may have been conjointly produced by selection, and that the winter pelage and the long limbs of the Mountain Hare may possibly be referred to a similar origin (pp. 197-202), in short, that selection may sometimes be operative on two or more characters concurrently. But as we cannot believe that the bulk of specific differences are the result of individual acts of selection and adaptation, we must fall back on the possibility that they are correlated with characters modified by selection. Of this we have, as has been stated, very scanty direct proof. It is necessary, then, to examine the various causes of correlation and ascertain if they are of such a nature as to render it likely that, if, for example, two characters are thus associated, selection acting on the one is likely to modify the other.

Of the various modes of correlation outlined above (p. 228 and following), I believe that those involving a reciprocal or a unilateral dependence of characters on each other may very well be of importance as a factor in Natural Selection. Here we have a causal connection between the characters of such a nature that, as the one character (in a case of unilateral dependence) is modified by selection, so will the other be modified as a result. But when the association is simply coincidental (or " static ", Dürken), it does not seem to follow that alteration of the one character will be accompanied by a similar alteration of the other. It is quite true that, if selection is operative on a stock in which, for example, the factors for two characters (A and B) are linked, the preservation of the individuals bearing character A will tend to ensure the perpetuation of character B ; and also that according as variations of A are selected (A^1, A^2, A^3 . . .), so will some variations of B be automatically selected. But if A is a useful character, *i.e.* one subject to selection, and B is not, the selection operative on A will only be successful in modifying B in a definite direction, if the mutants A^1, A^2, A^3 and B^1, B^2, B^3 are produced at the same time. We need not, of course, discuss the effect of selection operating on a population homozygous, for several characters. If all the individuals constituting that population survive some catastrophe in virtue of one of the characters they bear, the other characters will naturally be perpetuated as well. But progressive modification of such a population could only be effective if variants occurred which would obviously terminate the homozygous condition of the stock.

Static coincidence, then, does not seem to be a means of correlation whereby selection has often brought about the transformation of groups of characters. On the other hand, as we know little concerning what we have called physiological correlation, and as we are unable to say whether the points of difference between allied species are likely to have this basis of association, any discussion as to the effects of selection on such correlated characters is premature. It is of some importance to note that correlation due to the interdependence of the parts during ontogeny seems to diminish during growth (Jenkinson, *l.c.*, pp. 75 and 277).

We may conclude, then, that it is at present impossible to decide whether non-serviceable differences between species are likely to have been produced through correlation with serviceable ones. In the first place, the utility of slight differences is not easily demonstrated. Secondly, the basis of association in the very frequent cases of correlation is unknown, and therefore we cannot say whether selection could actually have any influence. Thirdly, when it is known, it is sometimes of such a nature as to be unaffected by selection. Lastly, actual evidence of such association in natural population and its modification by selection is deficient. It is clear from what has been said above that characters may sometimes be so associated as to render the assumption a justifiable one; and the evidence, on which Darwin relied, that in the course of agriculture and stock-raising certain characters have been correlatively influenced by selection, must be allowed to count for something. But we require far more plentiful instance before we can claim that the vast mass of apparently non-serviceable differences have been produced in this fashion.

At this stage it is appropriate to recall the fact that we have to deal (*a*) with groups that are connected by intermediates and are recognisable as species or races because certain character-associations are found more frequently (in more individuals) than others, and (*b*) with assemblages that are to be distinguished more readily one from another on account of some measure of discontinuity. I do not think that we need draw any fundamental distinction between these types as far as the causes which produce the correlation are concerned. If the high correlation and discontinuity seen in the latter type are produced by the selection of individuals having a certain set of attributes, the less absolute, though already perceptible, correlation seen in the first type (*a*) may be due to the fact that selection is only at its initial stages. The proof that discontinuity is actually produced by the selective elimination of individuals having a certain constitution depends rather on the general case we can establish for the effectiveness of Natural Selection than on any definite proof that in a given instance such intermediates were actually eliminated. The establishment of some measure of isolation will naturally promote and maintain such discontinuity. We must also be prepared to recognise that the correlation of characters may not depend on their adaptive value but on more intimate and fundamental causes. We have, however, little evidence to prove that correlation arising from these causes is ever so absolute as to produce discontinuity between different systems of variates.

(3) If we are inclined to question the efficacy of mass-transformation by the environment, and of Natural Selection in producing groups of the status of species when the characters distinguishing the latter attain a high degree of correlation, we should inquire whether it is possible to explain the origin of such correlation on the assumption that all hereditary change in a population is purely germinal and independent of Natural Selection as far as the multiplication of individuals exhibiting such change is concerned.

Is there any theoretical reason why we should not simply assume that the groups of individuals with differentiated characters represented by species simply arise by the successive appearance of variations first in one part and then in another of the population, always provided that such individuals find a suitable opportunity for spreading (see p. 219)? I ought perhaps to repeat the statement made in the last chapter that whatever disabilities may be attached to the theories of mass-transformation by the environment and Natural Selection they at least supply plausible explanations for the multiplication of individuals carrying new characters, whereas any theory that attempts to dispense with them leaves this question very largely " in the air ".

If we are tempted to assume that the characters distinguishing a species or a race arose successively through an alteration in the germinal constitution of a parent stock, and with unlimited time at their disposal spread through an entire population, we thereby increase the difficulty already pointed out (p. 220 and following) of explaining how the individuals carrying these characters can multiply, for we now must explain the spread, not of one non-adaptive character, but of several. If by a lucky coincidence a " mutant " form A'BCD arose in a species ABCD and was able to spread by occupying an untenanted habitat, it might come to be numerically well-represented. But let us suppose we have to account for the origin of a species A'B'C'D' on these terms. We have now to provide a means whereby the variants representing the next step, A'B'CD, may multiply, and so on for the remaining steps. I think it would be easier to accept this method of accounting for the origin of more or less homogeneous groups, if it could be shown that change in several characters occurred simultaneously; for then we would have to account for the spread of one set of individuals, *i.e.* our A'B'C'D' individuals of the above example. We might be tempted to derive our homogeneous groups from a limited number of individuals of both sexes in which all the distinctive characters appeared simultaneously. That characters may be *associated* in heredity is, I think, sufficiently proved by the evidence assembled on pp. 229-233. But that they *originate en bloc* is not substantiated by convincing evidence.

In addition to a history and full treatment of the *Oeno-*

thera mutants (1917), Gates has collected a large series of records of " presumptive " mutations in wild and cultivated plants, and a smaller series for animals (1921, p. 55 and following). Apart from the *Oenothera* mutants many of Gates' records are "presumptive", *i.e.* the exact history is not known, and it is not certain if the forms actually have arisen *de novo.* The majority of the cases cited are of single-character mutation, though several characters are sometimes involved. It seems very doubtful, to say the least, whether the latter are of such advantage as to promote the spread of the mutant. Taking into consideration (*a*) the ambiguous nature of the origin of these forms, and (*b*) the greater frequency of mutation in single characters, I do not think that these records afford strong evidence for the origin *en bloc* of such groups of characters as distinguish species.[1] The evidence for the origin of such groups of characters in animals is even less convincing, and rests mainly on Crampton's studies of the *Partulas* of the Society Islands (1917). The " mutational " forms having new character combinations were obtained by Crampton, and are assumed to have arisen as such since the careful survey of the islands by Garrett in 1884. I think, however, that one should hesitate before assuming that Garrett's survey was exhaustive, or that the new characters arose *en bloc.*

As for the *Oenothera* mutants themselves, their origin is still contentious matter. There is, as is well known, a strong body of opinion that *Oe. lamarckiana* is of hybrid origin (to which the work of Davis lends substantial support), and that the new forms (*gigas*, *lata*, etc.) are merely recombinations of factors which appear in an intermittent fashion because of the peculiarly heavy mortality which occurs in *lamarckiana* pollen and seeds.

This argument has been rebutted by Gates (*l.c.*, p. 22), who points out that mutations have occurred " in such well-authenticated and self-pollinated species as *Oe. biennis* ". It is not stated, however, whether such mutations involve

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[1] It is likely, however, that "*en bloc*" mutation does often occur; but it is very difficult to argue from this to high correlation in a given population.

several characters. As for the view that the *gigas*, *lata*, etc., mutants are of hybrid origin, even if this is true I do not understand why the occurrence of the " mutants " should be discredited as evidence on the origin of species. While we must obviously attach more importance to the origin of entirely new characters than we do to new combinations of pre-existing factorial material as the result of hybridisation, the latter must play an important part in giving rise to many of the combinations found in nature. If the *Oenothera* " mutants " are of this order, and even if, as I understand the position, their discontinuity may be partly produced by the high sterility and the elimination of many gametes, they may be regarded as valuable evidence on the effects of recombination. They cannot, however, if this view is correct, rank as evidence as to the origin of combinations based on new factorial material.

On the latter subject, and on Lotsy's special hypothesis of the origin of species through hybridisation, I have hitherto said nothing. There can be no doubt that there are very good grounds for believing that " novelties " may arise from the recombinations of pre-existing factors, and that actually, as in the Roses and Willows, new forms attaining the morphological status of species have been thus produced. Further instances may be found in Darwin (1875, ch. xv.). The diversity of means by which isolation is produced, less potent perhaps in plants and sessile animals than in motile animals, renders it unlikely that such an origin of new forms will be very frequent. Even if successful crossings were relatively common, the chances are not very high that forms differing from the parent types in possessing many entirely new characters may arise from factorial recombination.

It should perhaps be pointed out that even if we invoke linkage as a means of accounting for the correlation of non-advantageous germinal differences, we are still saddled with the responsibility of showing how the individuals bearing such linked characters can multiply. The remarks made above concerning the simultaneous origin of characters are applicable to those which are linked, viz. that we might more easily explain the multiplication of individuals in which several characters were linked by assuming that the latter arose simultaneously, but we have little or no evidence of the occurrence of the latter phenomenon.

As far as the physiological basis of correlation is concerned we are, as I have already pointed out, very much in the dark as to its incidence, and any discussion of its rôle in giving rise to species or races, when non-adaptive change is assumed to be involved, is at present as valueless as in other circumstances.

It seems, then, that not only is it very uncertain how individuals bearing non-adaptive characters can increase numerically without some adventitious assistance, but also that, when a homogeneous group of individuals differing from its near allies in several such characters is established, we are almost compelled to assume that the latter arose more or less simultaneously. Such a phenomenon seems to be limited to the production of novelties by recombination, although there is some suggestion in the history of plant mutants that entirely new characters may have arisen in combination. The " polymorphic " nature of many species that have been carefully studied relieves us of the necessity of accounting for a universal measure of high correlation. Nevertheless, there seems to be little actual proof that non-advantageous germinal change occurs in such a way as to give rise to high frequencies of association where many characters are involved.

I have attempted in this chapter to show that, if we use the three chief explanatory hypotheses of evolution in order to account for the origin of species regarded as groups which are differentiated from each other in several characters, we encounter certain special difficulties if the characters in question manifest a high degree of correlation. It may be held that I am exaggerating what is, after all, only an exceptional event, and that, however uncertain the origin of variation and the means whereby variant individuals increase in a population may be, the difficulties raised in this chapter are largely factitious. High correlation, one might argue, is not frequent enough to cause us much embarrassment, and the constitution of natural populations, as we know them, is more consistent with the sporadic and local effects of the transforming principle, whatever it may be. I do not think, however, that we can at present speak with any authority as to the relative frequency of homogeneousness or the reverse in nature, and, as long as we find high correlation reported as frequently as it has been, and as long as we encounter natural assemblages with an apparently uniform constitution in respect to certain characters, we must seek an explanation of this phenomenon.

Our survey has been confined to the processes that are currently believed to give rise to the differentiation of species and lesser groups. We have confined our attention to the slight divergences, principally in structure, that distinguish allied species and races, and we have neglected those larger aspects of morphology that are concerned with the history of organs and their progressive improvement or deterioration. Taking the narrower view and confining our attention to interspecific differentia, we may perhaps be inclined to believe that all such differences may be satisfactorily explained by one or the other of the theories just considered, or by them all collectively. On this assumption we must believe that the history of an organ such as the vertebrate eye, or of a group of animals such as the Cephalopoda or the Reptilia, consists of a number of small steps, some of which might be treated by the systematist as " specific ". We ought, before we conclude our inquiry, to ask if modification by the environment, Natural Selection or chance mutation can bring about the origin of complicated organs or those sustained and progressive evolutionary episodes which we see in the history of any of the great groups of animals. In short, if one of these principles, or all of them collectively, can produce the sort of differentiation which we have been studying, is there any particular difficulty in believing that, *e.g.*, a complex organ is simply the end-term of a series of such change, each stage being more complex than the preceding one ?

We have, however, reason to doubt whether any one of these principles by itself and without very important modification constitutes a satisfactory explanation of the whole of the phenomena of evolution. It has even been suggested that they do not do so collectively, and that the evolution of complex organs on the one hand, and of certain evolutionary trends on the other, seem to require a special explanation. If that is the case, if such phenomena testify to the activity of a totally different evolutionary principle, may not the latter, held as it is by some to be apparent in the production of complex organs and orthogenetic trends, also intervene in the divergence of species? I do not say that need for this additional principle is proved or even required. There is enough evidence available to suggest that the current hypotheses, together with the effects of isolation, may be indeed valid explanations within the limits of our experience. But we cannot disguise the fact that they involve many difficulties and labour under many disabilities, so that we are bound to consider what alternatives have been proposed.

The doctrines of Natural Selection and transformation by the environment, whatever weaknesses we may detect in their apparatus of proof, supply at least a theoretical explanation of progressive modification. The doctrine of chance mutation (p. 247) must assume that, in any developmental series in which improvement or deterioration is perceptible, the successive stages in improvement, or the reverse, are brought about purely by chance without the intervention of any directive principle whatever; though an appeal is occasionally made to some physiological impetus (cf. p. 248).

(*a*) Darwin treated the origin of " organs of extreme perfection and complication " as one of the special difficulties encountered by his theory, and confesses that he felt the difficulty of explaining the origin of the vertebrate eye "far too keenly to be surprised at others hesitating to extend the principle of Natural Selection to so startling a length" (1859, p. 227). Perceiving that the chief difficulty lay in this, that " in order to modify the eye (*e.g.*) and still preserve it as a perfect instrument, many changes would have to be effected simultaneously " (*l.c.*, p. 226) he argues (1) that the modifications might be extremely slight and gradual and therefore not necessarily simultaneous ; and (2) that different modifications might serve for the same general purpose. Of these suggestions, (1) appears to be the most pertinent. Bergson (1911, p. 68) has, however, pressed the question further by inquiring how, if a variation is slight enough not to hinder the functioning of the eye, before the complementary variations in other parts necessary to make such a variation functionally advantageous were developed, it can be preserved and retained by Natural Selection. Its utility is not apparent during such a time, and while it is, as it were, waiting for the complementary variations, there is no reason why it should be of survival-value to its possessor. Bergson further points out that Mutation does not help us to explain this difficulty any more effectively. If the variations in the various parts are of the order of " mutations " (in the original sense) there are indeed less stages to pass through, less difficulties of accommodation, but there is this difficulty—that we must explain how the parts of the eye " thus suddenly changed remain so well co-ordinated that the eye continues to exercise its function ".

I think that we may neglect the possibility that the "mutational" stages may be large and liable to introduce lack of co-ordination. But even if they are slight we are still required to show how the right degree of co-ordination is attained.

Morgan (1919, p. 268) has attempted to establish a relation between the phenomena of chance and those of evolution in such a way as to provide an explanation of the origin of complex structures that does not depend on any directive principle, either in the form of environmental stress or of internal impulse such as that invoked by Bergson.[1] His solution is that " the degree of development of any character *increases the probability* of further stages in the same direction ". He cites as an instance the fact that a race of men 5 feet 10 inches in stature is more likely, if the average

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[1] It is not clear from the content whether Morgan believes this principle of " increase of probability " can operate independently of Natural Selection.

size of a mutational stage is two inches, to give rise to a race 6 feet in height, than is a race of an average height of 5 feet. There is, however, no greater probability that the race of men 5 feet 10 inches in stature will reach 6 feet than that the race 5 feet tall will reach 5 feet 2 inches. Morgan's example is in itself a valid proposition ; but my friend and colleague, Mr. C. C. A. Monro, has pointed out to me that it does not illustrate the principle he sets out to prove, viz. that once a given stage is attained there is *an increase in* the probability that further modification in the same direction will take place. Of course Morgan may not mean this. He may wish to imply that once a step has been achieved in a given direction it will afford a basis for a new step in the same direction. Once our race of men has attained a height of 5 feet 10 inches, it is likely that they will advance to 6 feet at the next mutational period. But this is not necessarily true, for there might be a decrease in stature, the latter being just as likely as the increase. In short, all that Morgan proves is that, *if mutations are in the same direction*, the race of 5 feet 10 inches may possibly give rise to one of 6 feet in stature. Of course Morgan is at liberty to reply that the normal operations of chance give us sometimes, *e.g.* in tossing coins, a " run " of one sort, and when we find a sustained series of mutations in one direction, they correspond to a series or " run " of " heads " or of " tails " obtained in tossing coins. I believe that there is some evidence of the occurrence of such " runs " in the data on variation ; but when we reflect that in complex organs many " runs " must coincide in order that the various parts may be co-ordinated (as pointed out above), it must be conceded that an appeal to chance is highly unsatisfactory. An appeal to Natural Selection or to an *élan vital* is a far slighter strain on our credulity than the reliance on chance in such circumstances.

We perhaps should notice that other geneticists are prepared to supply different explanations of progressive mutation. Thus la Rue and Bartlett (1918) are evidently inclined to account for the latter phenomenon in *Oenothera* by some principle of physiological momentum.

The progressive complexity of an organ is equally difficult to explain on the assumption that the transforming agency is some environmental factor. We may very well imagine that the progressive intensification or reduction of a stimulus may lead to a similar increased or decreased reaction or accommodation on the part of a structure. Progressive intensification of light may lead to the deepening of a pigment, and its progressive reduction may be followed by progressive loss of pigment. But it is almost impossible to imagine how, for example, continued exposure to light can lead to the actual complication of the vertebrate eye, *i.e.* to the addition of special parts and finer co-ordination.

How, again, on this hypothesis are we to explain the origin of (*e.g.*) one of the more complex types of Lamellibranch gill, with its ciliated discs, chitinous skeleton, junctions and folds? We may refer the complexity to the habit of feeding on certain types of food-particles, or relate it to a mode of life in progressively denser bottom-debris. But even if we could produce the proof of correlation between habit and structure, can we believe that the actual stimulus of food-particles of a certain type or mud and debris of a certain density thus demonstrated produced such structures as the ciliated discs, skeletal supports and the elaborate folds?

(*b*) The occurrence of "orthogenetic" trends is by now well known. The concept was introduced by Neumayr (Mutationsrichtung) for series of fossil Invertebrata, and has been repeatedly invoked in paleontological studies. As Cuénot (1925, p. 63) has pointed out, the notion is familiar to zoologists, inasmuch as living species or genera may be frequently arranged in series illustrating some principle of increasing complexity or regression (cf. Gadow, 1905). Two things must be made clear concerning such series. (1) Orthogenesis, Momentum, Rectigradation—the various phrases by which such series are indicated—are at present merely names by which we indicate a certain type of evolutionary phenomena. They are not explanatory hypotheses. (2) The importance of such series is not that they seem to have a sustained direction, but that the series is passed through without any apparent reference to Natural Selection. If such series could be related to progressive intensification of competition, or shown to be adaptive with reference to special conditions of life, the significance of the series as such would disappear.[1] Until the special circumstances of each case are reviewed, and the conditions of life and competition involved therein fully understood, many of such instances must be regarded as *hors de concours*. The instances of this process, however, that do impress us as evidence of such a momentum are those in which excessive, and almost morbid, complexity is attained, or a seemingly irrevocable history of simplification, or degeneration, is indicated. This may be seen in the history of the Ammonite suture, in the general course of Cephalopod phylogeny, in the special cases of extravagant growth and heavy armature (called "Momentum" by Dendy, 1912) in the evolution of certain types of pattern (as in the Swallow Tail Butterflies described by Eimer). Equally significant is the fact that the same complex evolutionary series may be passed through in allied groups. This phenomenon is recorded by Lang (1921, p. xvii. and *passim*) in Chilostomatous Polyzoa, and it is very important to note that "all stages of this history may occur simultaneously in different lineages under presumably the same environmental conditions". I do not think any one will claim that these phenomena have been so exhaustively studied as yet, that we can confidently assign a cause to them. In the present state of our knowledge, however, the species which figure as stages in such series appear not as accidental and individual steps, in either a purely fortuitous chain of events, or progressive adaptation, but as stages in the development of an impulse.

An instance of an orthogenetic trend in which I think the possibility of adaptation can be ruled out, is seen in the course of Cephalopod evolution. In this group of Mollusca, there has been a persistent tendency for the mantle aperture, which in the primitive types is widely open, to become re-

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[1] Lull (1917) makes the same point, drawing attention to the distinction between orthogenesis and "orthoselection".

stricted by the fusion of the edge of the mantle to the tissues of the head. In *Nautilus* the mantle-edge is permanently open. In the majority of the Decapoda, as is well known, there is on either side of the funnel an adhesive organ, formed on the stud-and-socket principle, a knob or ridge on the inner side of the mantle, fitting into a socket on the head, by which the mantle rim can be temporarily fixed to the latter. In two genera of Egopsida, however, *Grimalditeuthis* and *Symplectoteuthis*, there are permanent " infundibulo-pallial " sutures at these points, and in the Egopsida Consuta the sutures are deeper and the closure of the mantle aperture more extensive. In the Octopoda, the same process is at work in a different fashion. In these animals, there is a feebly developed adhesive apparatus of a different plan ; but the mantle aperture becomes restricted by the progressive fusion of the pallial and cephalic tissues at its outer ends, until it eventually, in the majority of the Cirroteuthidae, closes completely, leaving the funnel projecting, and in the Opisthoteuthidae the latter organ is overgrown and fused up with the original mantle-edge, its aperture alone persisting. In *Amphitretus*, however, the Decapod tendency is seen, as the open mantle aperture in this genus is restricted by a median fusion with the funnel.

It may be argued that this restriction of the mantle aperture in the Dibranchiate Cephalopods is (*a*) not devoid of adaptive significance, and (*b*) that it is not a general tendency shared by the Decapoda and Octopoda alike, but a separate event with a different significance in each group. It might be claimed that in the Decapoda, many of which are active swimmers, it aids locomotion by enabling a greater part of the water contained in the mantle cavity to be kept under compression in the cavity, and ejected through the funnel, instead of pouring out of the widely gaping mantle aperture. In the Octopoda, on the other hand, in which the progressive closure of the latter is more apparent in deep-sea forms, the closure might be regarded as a means of keeping the gills free from silt. Against both of these suggestions there are powerful arguments. In the first place, the development of permanent and extensive sutures among the Decapoda attains its maximum frequency in planktonic floating forms like the *Cranchiidae*, not in the active, powerful forms like *Architeuthis*. With regard to the Octopoda, it is very unlikely that the closure could succeed in keeping the gills free of silt, as water is admitted through the funnel aperture, and in any case several deep-sea forms have partly open mantle apertures. In the present state of our knowledge of these animals, the process seems devoid of any utilitarian significance, and to be a general progressive tendency manifested in different ways by the two main groups of Dibranchia.

The lack of satisfactory evidence in support of the three chief evolutionary hypotheses has induced many writers to reject them, and to fall back on a belief that organic evolution is the expression of some immanent capacity of will possessed by living organisms. Others have discerned a continuation in the world of organic beings of simpler forms of chemico-physical change, characteristic of more inert substances. I do not believe that we are as yet able either to refute these views, or to assign their correct value to the more orthodox theories of evolution. Until the cause or causes of variation in animals and plants are known, and the means whereby variates are correlated are fully ascertained, we must remain in the realm of conjecture. We do not know yet if modifications induced in the germinal material by the environment alone are heritable, whether environmental stimulus is necessary for the full expression of automatic germinal change, or whether the latter alone and unaided is the source of variation, nor is it yet clear how changes of one or the other of these types can become characteristic of whole populations by the multiplication of the individuals manifesting them.

The efficacy of Natural Selection is uncertain. There is circumstantial evidence in its favour, which in special cases amounts almost to proof. We have no evidence as to how new variants may multiply (*a*) if they have no advantage in competition, or (*b*) are not produced *en masse*. The means whereby variant characters are correlated in populations requires fuller investigation. The effects of isolation are sufficiently demonstrated, but their importance is secondary, for they do not account for the origin and dispersal of variants in a population, though their rôle in promoting divergence is undeniable. If, on the other hand, we are impressed by the evidence that there is a directive impetus of some kind at work in the correlation of the different parts of animals and plants, we have still to treat such an impetus in terms of individuals exhibiting such tendencies, and to account for their dispersal and multiplication. The appeal to some inner momentum may assist us to explain phenomena not readily to be interpreted in terms of the orthodox theories of evolution. But along with the latter, such an appeal must be tested, as far as the origination of species is concerned, by exactly the same criteria as I have endeavoured to apply in the earlier part of this section. Viewed in their light, it seems as though the conception of an inner directive force encounters just the same difficulty as that which we met in considering the doctrine of chance mutation, namely, that we neither find evidence that whole populations are simultaneously transformed by this means, nor is it apparent how isolated individuals bearing new characters can increase numerically

APPENDIX

KAMMERER'S EXPERIMENTS ON THE INHERITANCE OF INDUCED MODIFICATIONS

A STUDY of the work of the late Dr. P. Kammerer must lead the unprejudiced reader to conclude that, whatever doubt there may be as to the value of the experiments on *Alytes*, it should not be allowed to vitiate the conclusions attained from those on *Salamandra maculosa* and *atra.* These experiments and observations were so protracted and were conducted with such care and attention to technical detail that they should be considered on their own merits.

(*a*) Experiments on the mode of reproduction of *Salamandra maculosa* and *atra* (*Arch. Entwick.-mechanik*, xvii. 1904; xxv. 1907).—Accounts of these have appeared in various technical and semi-popular works, and it is unnecessary to give the details. We may at once admit that an alteration of the mode of reproduction induced by experimental means was inherited in one subsequent generation, even when the members of the latter were given access to their normal conditions for reproduction. Bateson's criticisms (1913, pp. 204-6) seem to me to have a partial validity. He pointed out (1) that the number of modified individuals was very low, and (2) that such individuals did not show the modification with equal intensity. Nevertheless the general tendency in the F_1 animals was plainly to manifest the type of reproduction imposed on their parents. In the F_1 individuals there was also a tendency to revert to the original mode of reproduction when the normal environment was supplied (*e.g.* in the case of *Salamandra maculosa* some gilled larvæ were produced in the F_1 whose modified parents were given basins of water in which to breed). In short, as Bateson suggests, the animals seem to be easily deflected from the parental mode of reproduction. This question will be commented on shortly.

(*b*) Experiments in colour changes in *Salamandra maculosa* (*Arch. Entwick.-mechanik*, xxxvi. 1910).—Here we observe a colour-change induced in the parent animals reappearing in F_1 and F_2 offspring, due consideration being given to controls and the range of variation in nature. We see the same tendency for offspring which had been returned to the original environment to regain the colour which the parents exhibited previous to experimental modification. We also see in a most marked degree that colour-changes induced in animals kept on a given background and in a given degree of humidity are progressively amplified, if several successive generations are kept in the same experimental conditions. Kammerer unfortunately does not state how many animals in each experiment were modified, nor the precise degree of modification in each individual.

If these experiments are accepted as properly conducted and planned, which I see no reason for doubting, we must grant (1) that an induced modification can be inherited, and (2) that it tends to become progressively weaker if the experimental subjects are exposed to a different set of conditions.

I do not doubt that what Kammerer obtained was an *accommodation*, and not a permanently heritable effect. An objection to Kammerer's results was raised on this score in the first instance by Baur. But are we entitled to draw a rigid line between *accommodation* and permanently heritable change ? May there not be a " threshold " stage in the acquisition of a fixed hereditary property ? It seems that a somatic modification induced by the environment may be transferred to the germ cells but in a labile condition, so that, when the stimulus that evoked the change is relaxed, the germinal change is gradually obliterated. If we believe that the main object of evolutionary inquiry is the origin of hereditary stable characters, then we shall conclude that the history of hereditarily unstable change is relatively unimportant. But if the work of Kammerer (and indeed that of Agar (p. 171)) has not established the origin of fixed hereditary properties, it has at least suggested that a " threshold " stage may exist in the establishment of new hereditary characters of environmental origin. It should finally be noted that, if Kammerer's own view of the inheritance of colour change in *Salamandra maculosa* be accepted, that change cannot be regarded as due to " parallel induction", but to an actual transference of a somatic modification to the germ cells. The same result is claimed (on evidence that is difficult to refute) by Dürken (*Arch. mikr. Anat. Entwick.-mechanik*, 99, p. 222, 1923).

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