ANIMAL CYTOLOGY
&
EVOLUTION

BY

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PREFACE

During the twenty years which have elapsed since E. B. Wilson's great work, *The Cell in Development and Heredity*, was written the science of animal cytology has advanced so much that a general text-book covering all branches of the subject would have to be three or four times the size of the present volume. Moreover, it is doubtful if any living cytologist is fully conversant with cell-physiology as well as with genetical and evolutionary cytology.

This book deals, therefore, with only one aspect of animal cytology, namely the evolution of the chromosomes. Since these bodies are themselves the material basis of evolution, when we study the changes which have taken place in them in the course of phylogeny we are, in fact, studying the evolution of the evolutionary mechanism itself. Thus the book might have been called 'The Evolution of Evolution', but such a title might have appeared ambiguous to some and pompous to others.

Such a large amount of genetical and cytological work has now been carried out on the flies of the genus *Drosophila* that 'Drosophily' has almost become a separate branch of biology. In one way this is all to the good, but in practice it often leads to a division between *Drosophila* workers and general cytologists or geneticists working on other groups of organisms. Thus the former are frequently ignorant of the not inconsiderable amount of cytological work which has been carried out on Orthoptera, Vertebrates, etc.; while, conversely, those who have worked on the cytology of grasshoppers or mammals are often woefully ignorant of *Drosophila* genetics.

There can be no doubt that this separation has had unfortunate consequences. For example, it was not realized until 1934 that the salivary gland chromosomes could be used for cytogenetical analysis in *Drosophila*, although these relatively enormous chromosomes had been studied in other dipterous flies as early as 1880. Had the first generation of *Drosophila* workers known of the work of Balbiani, Carnoy, Alverdes and others on the salivary chromosomes of *Chironomus* it is probable that they would have made use of the salivary chromosome technique in their own work twenty years earlier. If the present book helps to close up the cleavage between *Drosophila* workers and general cytologists it will have served one important purpose.

Any book written in war-time, when libraries are difficult of access, must suffer in some respects. If any cytological work of importance was carried out in enemy or enemy-occupied countries in the years 1940–4 it does not figure here because the author was unable to obtain continental journals after the fall of France. Moreover, certain rare journals were evacuated from London at the outbreak of war and were not available for reference. More serious was the fact that almost the entire book was written in North Wales, with only occasional visits to Oxford or London to visit libraries.

I am greatly indebted to a number of persons who read the manuscript and pointed out errors or made suggestions for its improvement. In particular I should like to thank Prof. Th. Dobzhansky, Prof. J. B. S. Haldane, Dr S. Hughes-Schrader, Dr J. S. Huxley, Dr U. Philip, Prof. Franz Schrader and Dr H. Spurway.

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CHAPTER I

INTRODUCTION—THE NATURE OF THE EVOLUTIONARY PROCESS

The object of this book is to discuss the bearing of animal cytology upon the problem of the mechanism and processes of evolution. By cytology we mean nuclear cytology, since the evolution of the cytoplasmic constituents of the cell is an entirely different subject.

Most recent discussions of evolution have included both animals and plants within their scope. Thus in Darlington's *Recent Advances in Cytology*, Dobzhansky's *Genetics and the Origin of Species* and Huxley's *Evolution, the Modern Synthesis*, the evidence from botany and zoology is interwoven on nearly every page. Although it must be admitted that this 'synthetic' method of treatment has certain advantages, it is gradually becoming clear that the evolutionary processes of animals and plants differ in certain broad features, so that for many purposes they are best discussed separately. For this reason, and also for considerations of space, the present volume deals exclusively with animal chromosomes and animal evolution, work on plant cytology being only referred to when it has a direct bearing upon the principles of chromosomal evolution in animals.

The cytology of the Protozoa has been omitted for a different reason. While not denying the excellence of much recent work on the nuclear cycle in unicellular organisms (e.g. that of Bělař (1926) and the more recent work of Geitler (1942), Chen (1940 *a*, *b*) and others), it must be doubted whether the time is yet ripe for a general discussion of chromosome structure or of the mechanism of evolution in the Protozoa and Protophyta.

The problem of how and why related species of organisms have acquired visibly different chromosome sets is one that has occupied the minds of cytologists for many years. On the other hand, it is an aspect of organic diversity which has been very much neglected by those who have written on the general theory of evolution. Yet as long ago as 1905 McClung spoke of advances in fundamental knowledge coming about 'by a comparison of the germ cells and body characters in nearly related species, by observing the differences in germ cells of individuals that vary from the type of the species, or finally by experimentally disturbing the normal conditions in the germ cells and observing the effects upon the body'. What McClung had in mind was clearly a somewhat premature hope that it would be possible to establish direct correlations between visible differences in chromosome morphology and the external structural characters used in distinguishing species. This expectation has been realized in part, but it is now evident that the architecture of the chromosomes is so complex that many of the evolutionary changes which occur in them are on a molecular scale and hence far below the limit of resolution of the microscope.

It is now generally agreed that all evolutionary transformations have had their origin in the chromosomes, and that these bodies which constitute the physical basis of heredity also furnish the material for the evolutionary process. Although Lamarckian or near-Lamarckian theories are still occasionally met with, particularly in the writings of some palaeontologists and bacteriologists, they are not put forward by persons who are well acquainted with modern work in the fields of genetics and cytology.

So far as we know at present there are only two kinds of events which are capable of giving rise to heritable changes and hence to evolutionary transformations: gene mutations and 'structural' chromosomal changes which involve alterations in the sequence of the genes. Cytoplasmic inheritance, which seems to play a role though a very minor one in some plants, is almost and perhaps completely absent in animals above the level of the Protozoa; it can safely be neglected in a general discussion of animal evolution.*

McClung's three lines of investigation: (1) comparison of chromosome sets in related species, (2) comparison between the chromosome sets of aberrant individuals and the normal set which is characteristic for the species, and (3) the experimental alteration of chromosome morphology, have all proved to be fruitful methods of inquiry, and have occupied the attention of many investigators. As early as 1914, Metz, in a series of classical papers (1914, 1916 *a*, *b*; Metz and Moses, 1923), was comparing the chromosome sets of different species of *Drosophila* and classifying them into groups according to the number and shapes of their chromosomes. Even before this, Wilson and other American workers had studied chromosomal variation in natural populations of Orthoptera, Heteroptera and Coleoptera (McClung's second line of investigation). It was not until 1927, however, that a reliable means of inducing chromosomal changes by experimental means was found. The discovery that irradiation by X-rays would produce both gene-mutations and structural changes (Muller, 1927) opened up vast new fields in both genetics and cytology. It made possible the formulation of precise 'laws' and principles governing the processes of chromosomal evolution. Until then it was hardly possible to relate the data of comparative cytology to the species problem. Before about 1930 most animal cytologists were more concerned with facts about chromosome numbers, sizes and shapes and with hypotheses about the mechanisms of mitosis and meiosis than with building their results into the general fabric of evolutionary thought. Thus for a time it appeared as if McClung's three lines of work had failed to yield results of general importance. For this reason chromosome cytology tended for a time to become an esoteric subject, the details of which seemed to

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* 'Maternal effects', i.e. an influence of the maternal genes on the cytoplasm of the egg, are quite common in animal genetics, but they have nothing to do with true cytoplasmic inheritance.

be of little interest to workers in other fields. Even to-day this tendency still exists to some extent, and many biologists seem to think of evolution almost entirely in terms of gene-mutations, neglecting the structural changes, or relegating them to a very subordinate part in their theories of evolution.

The rediscovery of the salivary-gland chromosomes in the Diptera (Painter, 1933; Heitz and Bauer, 1933) has entirely changed this situation. Once again, as in the time of Weismann, the chromosomes are coming to occupy the central place in physiological and evolutionary thought, only this time we know vastly more about their detailed structure and genetical behaviour in a great variety of animals and plants. By studying salivary-gland chromosomes it is possible to make direct comparisons between the gene-sequences of different individuals and species with an ease and precision previously undreamed of. It is now more than ever apparent that it is quite impossible to analyse the mechanism of evolution without taking into consideration structural rearrangements of chromosome parts. Theoretically, one might suppose that nearly related species might differ in a few genes, but that the sequences of their genes would be the same. In fact, this is not so, at any rate in the Dipterous genera *Drosophila*, *Chironomus* and *Sciara*, where the most closely related species always seem to differ, even if only slightly, in their gene-sequences.

The general view of evolution which is accepted by most modern biologists, and especially by geneticists, may be described as neo-Darwinian, since it lays considerable stress on the role of natural selection. It is sometimes objected that selection is merely a 'destructive' force, and hence cannot be expected to produce anything 'new'. But, as Huxley (1942) points out, all evolution is the result of an interplay between chromosomal changes and selection, in which the latter may be regarded as playing a 'directive' part, building up combinations of genes and gene-sequences which would not come into existence by mere chance.

The formulation of the mathematical theory of natural selection has been carried out in the past two decades by R. A. Fisher, Sewall Wright and Haldane. The examples worked out in their papers relate mainly to gene-mutations, but the same general principles apply, with few modifications, in the case of structural changes. One result of this theoretical work was to focus attention on the need for more precise data on the distribution of genetical and cytological variation in wild species, the size of natural populations, their fluctuations from month to month and year to year and other similar problems of *gene-ecology* and *population-dynamics*. In this book we shall not deal with gene-mutations, except incidentally, since our concern is with the cytological (as distinct from the genetical) aspects of evolution. It is, to be sure, almost impossible to draw any hard and fast line between cytological and genetic phenomena, but since the more strictly genetical side of evolution has been dealt with very fully from the neo-Darwinian standpoint in the recent books of Dobzhansky and Huxley it does not seem desirable to cover this ground once more.

It may be convenient at this stage to recapitulate the main elements in the neo-Darwinian position:

(1) Mutations and structural rearrangements are 'physico-chemical accidents' which are non-adaptive in origin (the various hypotheses as to the causation of these 'accidents' lie outside the scope of this book).

(2) Natural selection acts as a filter which eliminates mutations and rearrangements which are disadvantageous and favours those which are advantageous. The number of mutations and rearrangements which become incorporated in phylogeny is only a minute fraction of the total number which occur, the majority being disadvantageous.

(3) The probable effects of selection can be calculated mathematically if the physiological effects of the mutation or rearrangement and the population-dynamics of the organism (size of individual units of population, rate of reproduction, motility, etc.) are known.

(4) The spread or extinction of mutations which are neither strongly deleterious nor highly advantageous tends to obey the laws of chance. In small populations especially, disadvantageous mutations may spread and advantageous ones become extinct. Adaptation is thus never quite perfect.

(5) As far as we can tell at the present time all evolutionary phenomena can ultimately be interpreted in terms of gene-mutations and chromosomal rearrangements, polyploidy* and hybridization* on the one hand and natural selection and the laws of probability on the other, without dragging in any special principles which cannot be interpreted in terms of the above factors.

(6) No radical difference exists between 'macro-evolution' and 'micro-evolution'—the evolution of species and genera is a consequence of the genetical processes which are going on all the time in natural populations and does not depend on any unknown processes of an entirely different kind, as some authors (e.g. Goldschmidt, 1940) have supposed. Thus, as Mayr (1942) puts it: '...the origin of the higher categories is a process which is nothing but an extrapolation of speciation'.

The detailed evidence for these views has been set out by Dobzhansky and Huxley and will not be recapitulated here. Among the few recent authors who do not accept the neo-Darwinian viewpoint we may mention Robson and Richards (1936), whose discussion of the mechanism of evolution (not written from a genetical standpoint) ends on a note of complete scepticism and uncertainty, and especially Goldschmidt (1940). The latter author regards 'macro-' and 'micro-evolution' as entirely different processes, and believes that true species are formed in an abrupt manner by a mechanism entirely different from that whereby subspecies are produced. He thus rejects one of the fundamental principles of Darwinism, namely, that varieties (or at any rate some of them)

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* In animals these seem to play a very minor role, although in plants they are important factors in evolution.

are incipient species. Goldschmidt's views have been strongly criticized by Dobzhansky (1941*a*) and by Mayr (1942). The most complete answer to them comes from recent work on speciation in *Drosophila* (see Chapter VII). In this genus it has been shown that every gradation exists from 'strains' differing in a few quantitative characters only to fully developed species which are sharply demarcated from one another.

There are two main aspects of evolution: (1) the formation of species, and (2) morphological and physiological change. From a cytological standpoint we shall be interested in both of these. The differences in gene-sequence which distinguish one species from its nearest relatives throw a new light on the 'species problem', while the cytological characteristics of whole groups (haploidy of male Hymenoptera, absence of crossing-over in the males of the 'higher' Diptera, etc.) have a bearing on the differentiation of the larger groups and the problem of their evolutionary plasticity.

The term 'speciation' has been introduced into the literature of evolution to designate the process whereby new species come into being. Dobzhansky (1937*d*) has defined speciation as 'the fixation of discontinuity among organisms'. If taken literally, this definition would seem to include all kinds of evolutionary change, but Dobzhansky goes on to explain that by speciation he means the establishment of physiological isolating mechanisms which prevent effective interbreeding. Thus two 'races' which were originally capable of hybridizing freely are assumed to acquire either (1) a reluctance to cross-mating, (2) sterility of the cross, or (3) sterility of the hybrid. Any one of these three types of isolating mechanisms will prevent interchange of genes between the two strains and will initiate a new dichotomy in evolution.

It will be seen that speciation is conceived of as a rather special stage in the evolution of species—the stage during which the isolating mechanism is not yet completely effective, but is spreading through the area occupied by the new 'incipient species' and possibly becoming more efficient by selection of subsidiary 'modifying genes'.

A number of attempts have been made in recent years to define the concept of the species. One difficulty arises from the fact that taxonomists working on different groups do not necessarily have the same standards as to what should be regarded as a 'full' species. In particular, the criteria seem to differ greatly according to whether the group has been thoroughly studied or not. Thus, as Mayr (1942) puts it: 'The student of spiders may still have the species concept which the ornithologist had in 1880, and the student of weevils that of the ornithologist of 1900.' If species were nothing but morphological entities it would probably be impossible to frame a definition of the species which would apply in annelids, insects and mammals, since there would be no way of comparing degrees of structural divergence in groups whose morphology is so radically different. However, since species are, by common consent, biological as well as morphological entities, we may attempt to frame a biological definition.

It is this question of arriving at a satisfactory definition and applying it in practice that is referred to by museum taxonomists as the 'species problem'. Most of the definitions that have been put forward admit the gradual nature of speciation and adopt a dynamic attitude to the problem, recognizing that species are stages in evolution and not static entities. One of the most generally acceptable of the definitions that have been put forward is that adopted by Dobzhansky (1937*d*, 1941*a*), according to which species represent 'that stage of the evolutionary process at which the actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding'.

One objection to this formulation is that it defines the process of speciation rather than the idea of the species; another is that it is often difficult to decide whether two forms are 'physiologically incapable' of hybridization. Many forms can be crossed in the laboratory that probably never hybridize under natural conditions, and occasionally wild hybrids are encountered between forms that must be regarded as valid species from every other point of view. The present writer would prefer a definition somewhat more general in character: 'A species is a group of individuals which are capable of normally and regularly breeding together, except in so far as they may be separated by geographical isolation.' This formulation implicitly admits that absolute physiological isolation is not the essential criterion—the acid test is whether the two forms are able to interbreed 'normally and regularly'. Mayr (1940) has adopted a somewhat different wording that expresses the same idea: 'A species consists of a group of populations which replace one another geographically or ecologically and of which the neighbouring ones intergrade or hybridize wherever they are in contact, or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers.' The general adoption of this viewpoint in ornithology has led to a considerable reduction in the number of species recognized by taxonomists, many forms which were earlier looked upon as full species being now regarded as geographical subspecies. But in many groups of insects the adoption of the new 'biological' outlook in systematics has led to an increase in the number of species, by revealing the existence of 'cryptic' species so similar in outward appearance that the old-fashioned taxonomist would never have regarded them as specifically distinct, although it is now clear that they form entirely different breeding units.

The chief feature that all these definitions have in common is the recognition of the species as a *breeding unit*. Admittedly, this concept is not much use to a museum taxonomist faced with a tray of pinned insects or a drawer of stuffed birds, but it is to be hoped that it will eventually be applied in all cases where an element of doubt exists as to the specific distinctness of two forms. In cases such as the head and body lice of man (originally described by Linnaeus as distinct species but regarded by modern authors such as Buxton (1940) as races or subspecies) the essential thing is to determine whether one or two breeding units are present.*

Sturtevant (1942) has laid down three criteria for deciding whether a given form should be regarded as a distinct species:

(1) 'Distinct species must be separable on the basis of ordinary preserved material.'

(2) 'Cross-fertility between distinct species is in general absent or so slight as to make unlikely any transfer of genes from one to the other in nature.'

(3) 'Subspecies usually replace one another geographically, species may do so, but are more likely to show extensively overlapping distribution areas.'

The first criterion would be acceptable to most museum taxonomists but probably not to all geneticists. The third one has many exceptions, but may be useful in doubtful instances.

The idea that species are artificial categories created by man out of a disorderly array of intergrading forms is one that is only occasionally expressed, although it occurs in the discussions of some palaeontologists and in the writings of some biologists whose work has been concerned with asexual organisms such as bacteria, in which it is quite possible that true species do not exist. The fact that there is a 'species problem' does not necessarily imply that species are not perfectly real and natural entities; it merely signifies that taxonomists sometimes disagree about the labelling of museum specimens and that the 'species' they create are sometimes artificial. But this artificiality (where it occurs) is not inherent in the material; it is due either to human failings of the taxonomists themselves, or to the small number of specimens available for study, or to the fact that most new species are described on a few morphological characters, without any biometrical, ecological or zoogeographical studies.

In spite of all these difficulties it is really remarkable how much unanimity exists about the delimitation of species in groups that have been adequately studied. The birds are possibly the best example, from this point of view; there are only about 8,500 species known in the world, and it is probable that less than 100 new species remain to be discovered (Mayr, 1940). Moreover, the number of taxonomists who have specialized on birds is relatively very large, and, as a result of the labours of collectors and sportsmen, museum collections of birds are far more complete than is the case in most other groups. This situation may be compared with the lamentable state of affairs in many groups of insects, where the known species represent only a small fraction of the total

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* Obviously, none of the definitions of the species quoted above apply in the case of obligatorily parthenogenetic forms. A re-investigation of the 'species problem' in such forms is badly needed.

number existing in the world. Where, however, we are dealing with insects that have been very extensively collected (such as the larger and more decorative butterflies) we find that there is a general unanimity as to the delimitation of the species, which are just as definite entities as in the case of birds.

Mayr estimates that only about 1% of the 8,500 species of birds are 'difficult species' which are so similar that competent authorities have real difficulty in separating them. A considerably larger number, however, seem to have reached a stage in evolutionary differentiation at which it is difficult to decide whether they should be regarded as 'full' species or not. Out of 755 species indigenous to the North American continent Mayr estimates that 94 ($12\frac{1}{2}$%) represent 'species in the making'. Some of these forms are readily distinguishable, but in their general morphology they indicate clearly enough that they have only recently broken off the parent species; for the most part they seem to be geographically isolated forms confined to small areas in the Rocky Mountains or to islands off the Californian coast. The existence of these 'incipient species' (which may be compared with the A and B races of *Drosophila pseudoobscura*) is a confirmation of the dynamic view of speciation outlined above and an argument against the view that it will eventually be possible to decide on the delimitation of *all* species with complete certainty and unanimity. The situation is, in fact, just what one would expect if the origin of species is a gradual process. On the other hand, if Goldschmidt's viewpoint, according to which species arise by sudden 'macromutations', were true we should not expect to find all gradations between races and species existing side by side in nature.

If we could represent the exact phylogeny of every group by a diagram in the form of a branching tree, it would be evident that the trees were not all the same shape. Some groups have branched out into a vast number of species while other phylogenetic trees have few branches situated far apart. In many families one large genus includes about 90% of the species, the remaining 10% being placed by taxonomists in a large number of much smaller genera. In some groups the morphological differences between species are relatively slight, while in others they are obvious even to the superficial observer. The evolution of each group may be regarded as a 'pattern', of which the existing species and subspecies represent a cross-section.

With the development of scientific taxonomy the need for a more elaborate terminology than the usual hierarchy of species, genus, family, etc., has gradually become apparent. In groups that have been thoroughly studied by taxonomists such as the birds, mammals and Lepidoptera, many species seem to consist of a number of geographical races or subspecies which replace one another geographically. Rensch (1929) has applied the term *Rassenkreis* to complexes of forms replacing one another in this way. Huxley (1942) uses the term *polytypic species* in almost exactly the same sense. Where a number of entirely distinct species replace one another geographically Rensch speaks of an *Artenkreis*.

Obviously, a Rassenkreis can be thought of as gradually evolving into an Artenkreis by an increase in the differences between the subspecies until they eventually attain the status of full species. On the other hand, discontinuous and overlapping distributions are often found in closely related species, so that the Artenkreis principle is of less general application than that of the Rassenkreis. Mayr uses the term *superspecies* as equivalent to Rensch's Artenkreis.

These concepts have been applied mainly to the higher vertebrates. In insects, where the territory of the individual is so much smaller, ecological replacement is probably more important than in vertebrates, so that 'ecological subspecies' or 'biological races' (see Thorpe, 1930) are relatively more common.

An interesting situation exists where each subspecies of a Rassenkreis is interfertile with those occupying adjacent areas but where the end-members of the series are incapable of interbreeding when brought together, either in the laboratory or as a result of their areas of distribution increasing until they overlap. Numerous examples of this state of affairs have been given by Rensch (1929), Kinsey (1936) and Huxley (1942). These cases present taxonomists with a difficult problem of nomenclature. The differences between *A* and *B*, *B* and *C*, *C* and *D* may not be sufficient to warrant specific rank, but if *A* and *D* are not only very different in appearance but are completely infertile when crossed, what is the taxonomist to do? The only satisfactory solution in most of these cases would be to speak of each 'ring' or 'chain' of races as a Rassenkreis, the end-members of which are recognized to be genetically isolated. Kinsey (1936, 1937*a*), who has made an extremely detailed taxonomic survey of the gall-wasps (Cynipidae) of the U.S.A. and Mexico, has adopted the alternative of calling every morphologically distinguishable form a species, no matter how slightly it differs from its neighbours in the chain. His 'species' are thus not equivalent to those of other authors; they correspond to the geographical subspecies, races or 'strains' of ordinary taxonomic practice.

In a later paper (1942) Kinsey has gone so far as to deny altogether the validity of the species-concept. Thus in one place he speaks of the 'nebulous something which everybody calls a species but which nobody can define, describe or recognize in a fashion which is quite acceptable to the next student in the field', and in another: 'Now we are ready to question the reality of any grouping of local populations, into species or any other category.' What Kinsey is really saying here is that every population has a distinct genetical make-up (a fact fully recognized by genetical writers such as Dobzhansky), and that in the 'chains of races' with which he has been dealing each geographical race intergrades with the next so that no definite discontinuity exists between them. The real gaps are, of course, between the entities which he calls 'complexes', but which we must regard as true species, although perhaps of a special type. When speaking of these Kinsey states that there is no interbreeding between them, and that 'sterility mechanisms have finally entered as primary isolating factors, at this taxonomic level'. It may be worth remarking, in passing, that the speciation pattern of the Cynipini may have been largely determined by that of the plant genus (*Quercus*) upon which they live. The fact that several species of *Cynips* may live on one oak is not an argument against this view, since the single species of tree may formerly have had a discontinuous distribution.

Although we may agree on a broad general definition of the species-concept it is undeniable that different types of species occur, often in the same group. Huxley (1942) speaks of polymorphic, polytypic and monotypic species (the first consist of sharply contrasted types, the second are differentiated into subspecies, the last are not differentiated). From a genetical and cytological standpoint an equally important distinction is between rare and common species. In general, common species are more variable than rare ones, as was realized by Darwin; but rare species are more likely to be split up into isolated groups between which migration seldom or never occurs. A further separation can be made between 'continental' species (i.e. those which occupy a continuous area of continental dimensions) and 'insular' ones (which occupy limited territories such as islands, mountains rising from a plain or desert, etc.). Kinsey (1937*b*) finds that in gall-wasps the 'insular' species are far less variable than the 'continental' ones (the latter being mostly common species, the former rare ones).

We still know very little about the cytological characteristics of rare versus common or continental versus insular species. Judging from *Drosophila* it rather seems as if the number of different gene-sequences is greater in species with a restricted distribution (such as *D. pseudoobscura*) than in ones which are world-wide (such as *D. melanogaster*, *D. funebris*, *D. simulans*, *D. hydei*, etc.). But the comparison may not be a fair one, since many of the cosmopolitan species owe their present distribution to human agency within the last few centuries. If it should really be the case that cytological variation is greater in rare, insular species than in common, continental ones, that would be extremely interesting, since all the evidence points to the relationship being the other way about in the case of genic variation. It may be that most gene-mutations which undergo fixation do so as a result of selection, while most gene-sequences which establish themselves do so by chance.

The general picture of natural populations that has been built up in the last few years suggests that in most species there is far more genetical than cytological variation; that is to say, the number of different gene-sequences existing at any one time is much less than the number of allelomorphic gene-differences. So great is the number of possible combinations of the latter that in man and domestic animals it is fairly clear that every individual differs genetically from every other one (except in the case of identical twins). Mayr (1940) believes that this conclusion holds true for all other animals (parthenogenetic forms excepted), but as regards the lower animals this is so far unproven.

On the other hand, in most species the number of cytologically distinct types is fairly small, although it may run up to several thousand if we consider all possible combinations of perhaps a dozen or more different inversions or other structural rearrangements. Even so, however, a large number of individuals will be cytologically identical, although they may be all genetically unique, as suggested by Mayr.

The importance of geographical isolation for the fixation of genetical and cytological diversity has been stressed by all modern writers on evolution. The subspecies, races or strains into which most species can be split up nearly always have distinct geographical distributions which may overlap or not, but are seldom completely co-extensive. In the higher vertebrates it is not unusual for a species to be divisible into several distinct geographical subspecies, while in insects we find all gradations between this situation and the one where several 'biological races' inhabit the same area but live on different hosts or food plants. We may infer from this that geographical and ecological isolation play a primary role in the differentiation of species into the lower categories of subspecies, races, strains, etc. While some of the gene-differences between these categories may be non-adaptive, there can be little doubt that the gene-complexes characteristic of geographical races and subspecies are, in general, adaptive to the particular conditions under which these forms live. Crossing between different geographical races or subspecies will necessarily break down these adaptive combinations of genes and will produce individuals less well adapted to their environment than either of the 'pure' forms (unless there is a complete gradation of environmental conditions, which will seldom be the case). Thus any isolation mechanism, whether physiological or cytogenetical, will usually be to the advantage of both forms. The production of new isolating mechanisms from time to time and their perpetuation through selection are thus seen to be essential to the preservation of stable, adaptive combinations of genes.

Before any mutation or structural rearrangement can establish itself in evolution it must first of all make its appearance in the progeny of a single individual and then undergo fixation in a local population or group of individuals. The probability of a mutation or structural rearrangement undergoing fixation, whether by chance or because it has a 'positive selective value', depends on the size of the population or, more precisely, on the *population number*, a concept of Sewall Wright (1931, 1932, 1935) for which he uses the symbol N.* The smaller N is, the greater the chance of a mutation or rearrangement being lost by extinction or reaching 'fixation' as a result of the extinction of alternative

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* N has been defined by Wright as follows: 'The conception is that of two random samples of gametes, N sperms and N eggs, drawn from the total gametes produced by the generation in question....Obviously N applies only to the breeding population and not to the total number of individuals of all ages. If the population fluctuates greatly, the effective N is much closer to the minimum number than to the maximum number. If there is a great difference between the number of mature males and females, it is closer to the smaller number than to the larger.'