THE
EVOLUTION
OF LIVING
ORGANISMS

A Symposium to mark the

Centenary of Darwin's 'Origin of Species'

and of the Royal Society of Victoria

held in Melbourne, December 1959

Edited by G. W. LEEPER, M.Sc.

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PREFACE

FOR THE ROYAL SOCIETY of Victoria, the year 1959 was a double centenary. It was a hundred years since Queen Victoria had granted the royal title to the Society, and a hundred years since the publication of Darwin's *Origin of Species,* which began a new era in science. The Council of the Royal Society decided to mark the occasion by holding a symposium on the general topic of 'The Evolution of Living Organisms'. Invitations to contribute were sent to all workers in the field in Australia and New Zealand as well as to selected overseas workers. This Darwin Centenary symposium had the co-operation of the University of Melbourne and the Australian Academy of Science. Financial help was also given from the Science and Industry Endowment Fund. The Council of the Royal Society of Victoria takes the opportunity here of again expressing its thanks to our helpers.

The scientific discussions were held at the Royal Society's Hall at 9 Victoria Street, Melbourne, from 8 to 11 December 1959. Dr Ernst Mayr, Director of the Museum of Comparative Zoology at Harvard College, was the official guest of the Society and he delivered the inaugural address in Wilson Hall at the University of Melbourne on 7 December. His address appears as the first chapter in this book. The address was a memorial to Oscar Tiegs, F.R.S., Professor of Zoology in the University of Melbourne from 1951 till his death in 1956. Professor Tiegs was for many years a Councillor of the Royal Society and had first suggested the organization of a centenary symposium. The chapter by Sir Gavin de Beer was an invited contribution from Great Britain. Those by Professor Westoll and Dr Baas Becking were delivered as evening lectures during the symposium. Sir Macfarlane Burnet's chapter consists of an address given at an evening meeting of the Royal Society of Victoria on 12 March 1959.

The remaining papers were presented at the full meetings of the symposium. These fall into two main groups. The first part of the book, relating to evolution in general, contains chapters 1 to 5 listed above, and 6 to 20 from the full meetings. The second part (chapters 21 to 36) is concerned especially with the fauna and flora of Australia and New Zealand. Authors' acknowledgments and some authors' summaries were regretfully deleted in order to save space.

My thanks as editor are especially due to Mr A. G. Willis, Senior Lecturer in the Department of Zoology at the University of Melbourne, who carried out a great deal of the editorial work during my absence from Australia in the first half of 1960.

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G. W. LEEPER
President, Royal Society
of Victoria, 1959-1960

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ACCIDENT OR DESIGN,
THE PARADOX OF EVOLUTION

ERNST MAYR

Museum of Comparative Zoology, Harvard College

W E ARE GATHERED on this occasion to honour the memory of three different events or persons: The hundredth anniversary of the granting of the Royal title to the Royal Society of Victoria; the centenary of the publication of Darwin's *Origin of Species,* an event of exceptional significance to Australians because it provides the key for the explanation of the unique fauna and flora of this island continent; and the memory of Oscar Werner Tiegs, one of the great zoologists of the past generation.

When asked to deliver an oration in honour of Tiegs' memory, I felt that no other topic would be more suitable for this occasion than that central problem of evolution, the problem of the origin of adaptation in the living world. Tiegs never lost sight of this central problem throughout his painstaking researches into the histology and development of aberrant groups of arthropods. When studying structural differences between myriapods and insects,' which he knew to have descended from a common ancestor, he always asked the question, 'By what steps did they follow their diverging pathways, and what factors controlled these steps?' A study of his major publications makes it very evident that he was vitally interested in the topic of today's lecture even though he himself never actually published on this subject. Tiegs' concern is not surprising, for indeed no other evolutionary problem is of equally broad interest to biologists and non-biologists alike. Once agreement is reached among biologists as to the solution of this problem, all other difficulties will solve themselves. It is the central problem of evolutionary biology.

The theory of evolution has come a long way since 1859. After a hundred years of controversy on literally every aspect of organic evolution there is now virtually unanimous agreement among the working evolutionists. This is true not only for the fact of evolution itself, but for many specific problems such as the major phylogenetic pathways, the genetic material of evolution, the multiplication of species, the role of isolation, and the rates of evolution, to mention merely a few outstanding aspects.

Without going into a detailed history of past disputes, let me try to summarize in a few words the synthetic theory of evolution as it emerged in the 1930s from a fusion of the best elements of the numerous conflicting

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theories. According to the synthetic theory, evolutionary change is due to innumerable small genetic changes, the success of which is determined by natural selection. Mutation and recombination produce an endless variety of genotypes, the survival of which is not random, but is at least in part determined by their 'fitness', that is by their ability to contribute to the gene pool of the next generation. It would be premature, however, to assert that this synthetic theory is now universally accepted. There are still some biologists who deny that natural selection can produce perfect adaptation. Even more widespread is the scepticism among natural philosophers who continue to insist that the evolutionary theory is unable to explain 'plan and purpose in nature'. Such doubt goes back to the beginning of the evolutionary theory. Darwin was fully aware of this difficulty, and in a letter to Asa Gray (26 Nov. 1860) he expressed the paradox as follows: 'I am conscious that I am in an utterly hopeless muddle. I cannot think that the world, as we see it, is the result of chance; and yet I cannot look at each separate thing as the result of design.'

Expressed in terms of the modern evolutionary theory, the paradox of evolution is the apparent contradiction between, on one hand, the seeming purposefulness of organic nature, and, on the other hand, the haphazardness of evolutionary processes. In order to understand the magnitude of this contradiction, we must look more closely at the two contradictory phenomena.

DESIGN

Let us begin with a contemplation of design in nature. Any biologist could quote literally hundreds of examples of the most incredible and miraculous adaptations. Let me mention only one or two.

The Yucca moth is specially adapted to the Yucca plant and depends on it throughout its life cycle (Rau, 1945). The Yucca plant in turn is adapted to be fertilized by this insect and by no other. The female moth collects a ball of pollen from several flowers, then finds a flower suitable for ovipositing. After depositing her egg in the soft tissue of the ovary, by means of a lance-like ovipositor, she pollinates the flower by pushing the pollen to the bottom of the funnel-shaped opening of the pistil. This permits the larva to feed on some of the developing seeds of the fertilized flower, and yet guarantees the development of enough seeds in the non-parasitized sectors of the fruit to permit the Yucca plant abundant reproduction. This perfection of the mutual adaptation of flower and moth is indeed admirable. Yet, in addition to this pollination and egg-laying relationship, there are numerous other adaptations, such as the emergence of the pupating larvae only after rain and the emergence of the moths in early summer some ten months after pupation, precisely at the time when the Yucca plants are in flower. 'Could blind chance have achieved such perfection?', ask the sceptics.

Or, let us take the field of intra-cellular symbionts studied by Buchner and his students. Here we have innumerable structures which permit insects and other metazoans to house the bacteria, yeasts or other micro-organisms,

which supply enzymes for the better utilization of the food of the host. Most of the host organisms have developed various mechanisms in order to supply their offspring with the right kind of symbiotic micro-organisms. The number of the sometimes almost incredible adaptations is legion (Buchner, 1953).

Or, let us take the division of labour and the harmonious collaboration of individuals of various castes in colonies of social insects, on which so many of our outstanding naturalists have reported in detail. Or, let us consider the orientation of nocturnally migrating birds. Even individuals which have been raised in complete isolation in order to eliminate the possibility of any form of learning are able to undertake a normal migration because they have not only a perfect clock mechanism telling them the time of the day and the season of the year, but they have also an innate knowledge of the stellar constellations which gives them the compass and the map by which to guide their wanderings (Sauer, 1957). As a matter of fact, we need not resort to such spectacular examples. There is a similar perfection in the various functions of the intestinal tract when it is digesting various types of food, or in the growing tissues of a developing organism. Whole books have been devoted to the discussion of such perfect adaptations and to what appears to be the extraordinary foresight of much of organic function and behaviour (e.g. Russell, 1945). Looking at all this, the conclusion is inevitable: we find in all organisms a fitting together of inborn actions or structures so perfect that one can hardly avoid such terms as 'design' or 'purposefulness'.

CHANCE

But when we ask how this perfection is brought about, we seem to find only arbitrariness, planlessness, randomness, and accident. Again let us study this in some detail. Any evolutionary change is brought about by a series of steps. The first of these is the change of a genetic factor, a mutation. The question whether there are any laws controlling the direction of mutation must be answered negatively. Mutations never seem to happen in response to a *need* for a particular genetic change, nor is a particular mutation released by a particular constellation of environmental factors. We still have a great deal to learn about the process of mutation; yet there is little reason to doubt that most mutations are merely copying-mistakes during the replication of the genetic material. Hence, it is correct to state that mutations are strictly accidental occurrences.

The next process of interest to us is the combining of genes (recently mutated or not) into genotypes. In sexually reproducing higher organisms these genes are organized in chromosomes. The reassortment of genes within the chromosomes, which normally happens once in every generation, is governed largely by chance. Each individual in sexually reproducing organisms has two homologous sets of chromosomes, one from the father and one from the mother. At some time prior to the formation of the gametes (the germ cells), the two homologous chromosomes exchange

equivalent pieces with each other by a process called 'crossing over'. By and large (there are many exceptions) no laws seem to determine where the chromosomes will break, or how large the pieces will be that are exchanged. The particular combination of pieces of maternal and paternal chromosomes making up the new chromosome that will enter a given egg or spermatozoon is largely a matter of chance, at least in most chromosomes and most species. Likewise it is largely a matter of accident *which* chromosomes will go into which germ cell, provided only that each cell receives its full set of chromosomes.

Chance is of overwhelming importance at the next step, the fate of the gametes. Each male produces millions or billions of spermatozoa. Only a few will fertilize eggs and contribute to the maintenance of the species; of the eggs likewise, not all will be fertilized. Since by far the majority of the spermatozoa and eggs are fully viable, it is again largely a matter of accident which will participate in the genetic contribution to the next generation.

Chance plays a far smaller role at the next step, the fate of the fertilized egg, or zygote, as the biologist calls it. Here we find a great difference between organisms like man, on one hand, which produce only a few zygotes, or on the other hand, certain parasites and marine organisms which produce millions. The greater the number of zygotes, the greater will be the mortality caused by pure chance; a whale feeding on planktonic crustaceans does not choose among them on the basis of their selective inferiority!

The series of partially or largely accidental steps leading to the production of a new potential parent can be listed as follows:

> Mutation at one or several loci.
> Crossing over.
> Distribution of chromosomes during reduction division.
> Success of gametes.
>> (a) Choice of partner.
>> (b) Choice of gamete.
> Success of zygote.

The fore-mentioned evolutionary events recurring during each generation are only a few of many such events completely or in part controlled by accident.

By now you will appreciate the true magnitude of Darwin's predicament. Nearly all steps leading to evolutionary change seem to be controlled entirely or largely by accident; yet the final product of evolution is perfection in adaptation. How can this seemingly hopeless contradiction be resolved? Many philosophers and even some biologists have adopted a defeatist attitude at this point and have abandoned all endeavour to find a causal explanation. Instead they have introduced a vitalistic or finalistic principle into their considerations, such as Bergson's 'Elan vital', Driesch's 'Entelechie', the 'inherent improvement drive' of some Lamarckians and similar euphemisms for the unknown. Others have appealed to saltation

as the source of the sudden origin of new perfections. Such capitulations to the unknown have had a paralysing effect on the spirit of scientific inquiry. They have proven themselves utterly sterile pseudo-solutions and are unanimously rejected by those who have a grasp of modern evolutionary theory and of modern genetics. Yet, a purely negative rejection of these pseudo-solutions is not enough. The evolutionist must come up with a constructive solution to the great paradoxical contradiction of evolution. What, then, is the solution?

Darwin emphasized again and again—and on this point he was in complete agreement with his opponents—that design cannot be the result of 'blind chance'. The choice of the expression 'blind chance' implies an explanation of evolutionary change by a single step, an all-or-none phenomenon. Such an explanation is in direct conflict with the synthetic theory of evolution, which considers any evolutionary change, including the perfecting of adaptations, as a two-step process. The first step is the production of genetic variation; the second step is the sorting of the many phenotypes into successful and unsuccessful (or less successful) ones. In the first step, indeed, blindness reigns, whether in the process of mutation itself or in recombination in its several aspects, from crossing-over to mate selection. It is here that occur the multiple blind accidents described above. Yet no damage is done by accident at this level, because the ultimate effect of all the accidents is to maintain high genetic variability. The less determinacy at this level, the less prejudging of probable fitness, the greater the ultimate choice for natural selection. The function of this first step is to keep the material of evolution variable—to keep pliable, so to speak, the clay which natural selection shapes into the finished sculpture.

Precisely the opposite is true for the second step, the evaluation of phenotypes. Here, where survival and differential reproduction are concerned, anything but blindness prevails. We have a proverb which is applicable here, 'Nothing succeeds like success', and this is the secret of natural selection. Success, in this case, means leaving offspring. But what is it that determines this success? If success were determined by blind chance, as are most processes that lead to genetic variation, we would not be justified in speaking of natural selection, for selection implies discrimination. But, and this is the cornerstone of the evolutionary theory since Darwin, it is justifiable to refer to differential reproduction as natural selection because individuals differ from each other in their genetic endowment, and it is, at least in part, the nature of this genetic endowment that determines reproductive success.

Merely asserting this claim dogmatically will not convince those who, until now, have been disbelievers. It is more important to point out that most of their objections are directed against obsolete views. No one can fully appreciate the strong position of the synthetic theory of evolution who is not fully aware of some of the recent improvements in our understanding of genetics and evolution. New findings in these areas have given us a much better insight into the working of natural selection. Let me demonstrate this through a discussion of (1) the nature of mutation, (2)

the relation of gene and character, and (3) the nature and object of selection.

MUTATION

The formerly held view that mutations are always drastic, and nearly always deleterious, has undergone considerable revision in recent years. This erroneous view was due chiefly to the choice of material by the early Mendelians, particularly De Vries, but was unconsciously favoured also by the working method of the classical geneticists, like T. H. Morgan, who quite naturally selected conspicuous and clear-cut mutations to study the laws of inheritance. Evidence is now accumulating that these mutations of classical genetics are by no means typical; indeed, they might well be in the minority. It is now believed that many, if not most, mutations have only slight effects or are entirely invisible because they affect only non-morphological characters. It would lead too far to present the detailed evidence for this assertion. It is based, in part, on a new concept of the gene, and he who would acquire a better understanding of the nature of mutation must investigate the nature of the mutating structure, the gene.

Within the last ten years, it has become firmly established that deoxyribonucleic acid (DNA) is the essential carrier of the genetic properties. Furthermore, it appears probable that the double helix of the DNA molecule serves as a complicated code of information which regulates the formation of the species-specific proteins and controls all development. Genes can be considered as the carriers of 'bits of information', to use the happy term of the information theory. Such bits of information are handed down from generation to generation, unless a mistake is made during their replication, and such a mistake is called a 'gene mutation'. The first mutation for which the exact chemical change has been analysed is that from normal hemoglobin to sickle cell hemoglobin (Ingram, 1956). There is reason to believe that the genetic information is contained in the precise sequence of the nucleotid pairs, and that mutation consists of a change in this sequence. However, no one so far has succeeded in working out exactly how this code operates.

Because all mutations segregate in a typically Mendelian manner, we treat mutations as a unit phenomenon. Actually it is quite possible (indeed, it is rather firmly established) that mutations are of many kinds so far as concern structure of the chromosome. Multiplicity of types of mutations is even more firmly established for the evolutionary significance of mutations. There is a broad spectrum extending from lethal and other drastic mutations to quite inconsequential changes of the DNA code. It is particularly important that many of these slight changes are almost equivalent in their selective significance, and that they result in no visible change of the phenotype. These are the genes called 'isoalleles' by Stern and others. An isoallele is the product of a mutation which represents not a breakdown of the physiological machinery, as mutations are so often visualized, but merely a slight 'variation on a theme'. This may lead to an alternate solution of a metabolic pathway. It may depend on the particular environ-

ment and 'on the particular genetic background on which such a mutation is placed whether or not it is superior to the gene from which it has mutated. The fact that an occasional mutation produces a superior gene must be emphasized in refutation of the widely held belief that mutation is always deleterious and destructive. The smaller the effect of a mutation the greater the probability that it will be advantageous. Microbiology in particular has taught us how often such mutations can be immediately constructive, for instance, in producing resistance to antibiotics or toxic substances. The recent work of Dobzhansky and his school, and of other population geneticists, has shown that even in higher organisms an appreciable percentage of mutations enhances viability. The picture we have of mutation in 1959 is certainly very different from that prevailing in the older evolutionary literature.

GENE AND CHARACTER

A second major revolution has occurred in our thinking about the relation of gene and character. In the early days of genetics there was the naive assumption of a one-to-one relation between gene and character: that each character is controlled by a gene and each gene controls a character. Accordingly, one spoke of the blue eye-colour gene, the red hair gene, the pink flower gene, etc. Such a concept of gene action led to the further assumption that each mutation was either favourable or unfavourable and, indeed, that mutation itself was the major evolutionary force. These assumptions permitted only one interpretation of evolutionary change; that evolutionary progress, dependent upon the opportune occurrence of favourable mutations, proceeds at the mercy of blind chance.

The modern picture is altogether different: a gene elaborates a gene product, added during development to the stream of differentiation. The products of innumerable genes collaborate to produce a terminal organ or character. Indeed, extremists have suggested, perhaps not quite seriously, that every gene affects all characters and that every character is affected by all genes. Clearly, it has become necessary to study gene *interaction* rather than gene action. Gene A may be deleterious when combined with gene B, but may grant superiority when combined with gene C. It is evident that this changed interpretation of mutation and of the genetic basis of the phenotype leads to an evaluation of natural selection entirely different from that of the earlier geneticists.

NATURAL SELECTION

An understanding of the working of natural selection is the key to the synthetic theory of evolution. I know of no other scientific theory that has been misunderstood and misrepresented as greatly as the theory of natural selection. First of all it is usually represented as strictly negative, as a force that eliminates, a force that kills and destroys. Yet Darwin, by his choice of the name selection, had clearly emphasized the positive aspects of this force. Indeed, we now know that one can go even further and call natural

selection a creative force. Secondly, natural selection is not an all-or-none phenomenon. The typologist, the follower of Plato, seems to think that alternatives are always either good or bad, black or white, worthy of preservation or doomed to rejection. This viewpoint is represented in two statements by well-known contemporary philosophers, chosen at random from the recent literature: 'Natural selection requires life and death utility before it can come into play'; and 'Unsuccessful types will be weeded out by the survival of the fittest but it cannot produce successful types'.

Actually, types in the sense of these statements do not exist; only variable populations exist. No one will ever understand natural selection until he realizes that it is a statistical phenomenon. In order to appreciate this fully one must think in terms of populations rather than in terms of types. There may be a thousand or several thousand variable gene loci in any species. Some individuals have more genes, some have fewer genes, which are favourable under particular conditions of the contemporary environment. The more favourable genes an individual has, the greater the probability that he will survive, and what is more important, that he will reproduce successfully. This probability of reproducing, of contributing to the gene pool of the next generation, describes the true nature of natural selection. And this is why natural selection is now often referred to as 'differential reproduction'.

We must emphasize at this point Darwin's genius in having recognized this point quite clearly. When speaking of the struggle for existence, he states in the first edition (1859) of the *Origin of Species,* that he uses this term 'in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny'. Since natural selection is a statistical phenomenon we must visualize it in terms of a population curve with a minus tail and a plus tail. Natural selection tends to clip off the tail of the curve with the minus variants in favour of the plus half, automatically resulting in a shift of the mean toward the plus end of the curve.

A further consideration will help to make the role of natural selection even clearer. Not the 'naked gene' but the total phenotype is exposed to selection. A gene occurring in a population will contribute toward very many phenotypes. In some cases these phenotypes will be successful, in others they will not. The success of the phenotypes will depend on the fitness of the particular gene, within the framework of the gene pool of this population. And this again will be an essentially statistical phenomenon.

Let us also remember that recombination, not mutation as such, is the primary source of the phenotypic variation encountered by natural selection. The usual argument of the anti-Darwinian is: 'How can an organism rely on the opportune occurrence of a favourable mutation whenever one is needed, considering that most mutations are deleterious? Surely all organisms would be doomed to extinction if in times of need they had to rely on such rare events?' Those who ask such questions confuse genetic variability and phenotypic variability. To be sure, mutation is ultimately

the source of all genetic variation. But natural selection operates not at the level of the gene but at the level of the phenotype. Further, the main source of phenotypic variation is recombination rather than mutation, and this source of variation is ever-present. With every individual differing genetically from every other one, every phenotypic character is variable, showing deviations of varying intensities and directions around the mean. Under normal conditions, selection will favour the mean (stabilizing selection), but if a deviation in any direction should be required by a newly arising selective force, the material is instantaneously available to respond to this force (directive selection).

Natural selection in this modern non-typological interpretation is an exceedingly sensitive instrument. The phenotype in nearly every case is actually a compromise between a number of conflicting selective forces. Let us take, for instance, the egg number in birds. On one hand there is a selective force to increase it upward because the larger the number of eggs, the more young will be produced. On the other hand, with young birds requiring parental care, there is an optimum number beyond which parental care deteriorates, so that the broods from the largest clutches actually have a lower survival than those from optimal clutches.

The almost unbelievable power of selection is demonstrated by much experimental work published during the last three decades. But even those unfamiliar with the results of experimental genetics need only to think of the products of animal and plant breeding to appreciate the power of selection. For instance, one might consider such physiological monstrosities as the modern dairy cow or some extreme breeds of dogs—all produced by selection!

I hope that this discussion will 'have made clear how unfortunate such terms as 'struggle for existence' or 'survival of the fittest' are, because they tend to distract our attention from the central aspect of the phenomenon of natural selection, its purely statistical nature. Anything adding to the probability of survival and reproductive success will automatically be selected for.

Evolutionary Accidents and Genetic Information

We are now ready to take a second look at the various levels of accidents discussed earlier. Taking into consideration (a) that most mutations have minor effects, (b) that selection deals with phenotypes and only very indirectly with genes, and (c) that all organisms live in a variable environment, it becomes quite apparent that there is nothing negative or deleterious about these accidents. All they do is to increase phenotypic variability or at least maintain it. They do not determine the course of evolution, they only supply the material with which natural selection works. With every species containing ten thousands, millions, or even hundreds of millions of individuals, genetic losses are not losses of evolutionary ground. They obey the rules of statistics, and gene frequencies will remain unchanged, as stated in the Hardy-Weinberg formula. On the contrary, these accidents lead to an unbiased method of testing whatever novel gene re-

combinations may produce superior phenotypes, particularly if there have been unprecedented or otherwise irregular changes of the environment.

This role of evolutionary accidents will become even clearer if we once more think of genes as carriers of information. Every genotype is a unique code of information which directs the development and the behaviour of an individual organism. Some codes lead to the production of phenotypes which, in the particular environments in which they are placed, are 'better adapted' than others. These we may call successful codes, and there is every probability that they will make a greater contribution to the gene pool of the next generation than will codes that resulted in less well-adapted individuals. The codes of information of the next generation will be formed from the gene pool, that is, from a recombination of the successful codes of the previous generation. These codes and the phenotypes they produce are statistical populations. Admittedly, recombination will result in the destruction of some perfectly satisfactory codes of the previous generation, yet some of the new codes may be in the plus tail of the curve and may be superior to anything that existed in the parental generation. The possible combinations of genes being infinite for all practical purposes, and with the fitness of the phenotypes to a large extent unpredictable (on the basis of parental genotypes), the undeniable role of accident in maintaining variation in populations is on the whole beneficial.

Objections to a Selectionist Interpretation of Adaptation

Numerous cases of adaptation are cited in the anti-Darwinian literature as defying a selectionist interpretation. The new understanding of the nature of genetic material and of the working of natural selection permits us to look at these objections in a new light and to test their validity. Let me select, among the many conventional objections, some that are typical of the arguments of anti-selectionists.

(1) *The Origin of Excess Structures.* This objection may be phrased as follows: 'How can natural selection be all-powerful if it permits the development of excessive structures that are either useless or definitely deleterious, like the antlers of the giant Irish Elk?'

The answer to this objection is at least three-fold: (a) the structure may actually have selective value at a certain stage in the life-cycle, for instance in the case of the young elk, or in certain environments; (b) sexual selection, as already pointed out by Darwin, leads to reproductive success, and is therefore favoured unless counteracted by other components of natural selection (and most of the 'excessive' structures cited in the literature are secondary sexual characters); and (c) what we see evolve is only the visible phenotype. The genes producing it may have been selected for other cryptic functions which contributed positively to the survival of its bearer. The wide-spread occurrence of the giant elk and its relative abundance indicate that in its particular environment, and at the time it lived, it very definitely had superior survival ability and was not handicapped by its giant antlers.

The possibility of cryptic contributions of genes to the phenotype bears also on the objection that many of the differences between related species seem to have no adaptive significance. 'How could natural selection have brought this about?', it is asked. Again, we must be certain that these characters have no adaptive significance, and if this should be proven, we must next determine what other functions the genes have which produce these so-called 'neutral characters'.

_(2) *Chance Mutations and Parallel Evolution.* This objection contends that chance mutations cannot be involved in adaptations which have been acquired repeatedly by separate evolutionary lines. How, it is asked, can unrelated organisms have had the same mutation in response to the same need?

This question confuses mutation and phenotype. It is indeed highly unlikely that parallel evolutionary developments have an identical genetic basis. Yet evidence is accumulating that similar phenotypes may be built up on a very different genotypic basis. Selection has an extraordinary power to steer variation in the right direction.

Evolution is strictly opportunistic and whenever a change of phenotype is advantageous, whatever aspect of the phenotype is variable at the time will be utilized by selection. Let us look, for instance, at the various structures which facilitate floating in marine pelagic animals. An illustration of such devices in various types of organisms shows that almost any part of the body may be used. Depending on the original variation of the particular genus or species which is shifting from a benthonic to a pelagic mode of life, various parts will be elaborated for the purpose of floating, that is, for the purpose of an enlargement of the body surface. The same opportunism is true for the plumes of the Birds of Paradise. The selective premium in this case is on conspicuousness, but it depends on genus or species whether the feathers of the crown, neck, flanks, wings, or tail are utilized for this purpose. A study of the eye in various types of organisms is a further illustration. The essential components of the eye are a light-sensitive tissue, a lens, a focusing device, and a pigment which shields the undesirable light penetration. Eyes have evolved in the animal kingdom at least a dozen times independently and the stated basic needs have been answered quite differently in each case.

(3) *Selection and Incipient Structures.* Another objection is based on the claim that natural selection cannot act on a newly developing organ until it has reached an elaboration that permits perfect functioning.

This claim overlooks several facts. Even a very rudimentary organ, like the first beginnings of a gliding wing in the 'Pro-avis', may be of distinct selective advantage provided that none of its enemies or competitors has the same or a more perfect structure. Again, as in previous cases, the incipient new character may be a pleiotropic by-product of a gene or gene-complex selected for a different reason. The new structure, although of no selective significance in the beginning, is in this case the product of the selectively advantageous total genotype. Furthermore, the acquisition of a new function may have given a pre-existing structure a new evolu-