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Retrospect of the Criticisms of the Theory of Natural Selection

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THE objections and difficulties felt in respect of Darwin's views seem to fall historically into four comparatively distinct periods; (*a*) the difficulties which he himself felt during the period when the theory was developing in his mind, all of which seem to flow from his acceptance of the blending theory of inheritance, as I have tried to make clear in the first chapter of *The Genetical Theory of Natural Selection*. There I discussed in particular the difficulty which he felt with respect to the maintenance of heritable variability in wild species, and point out that the problem is completely resolved, and the contradictory inferences to which it appears to lead are reconciled, when the "blending" is replaced by the "particulate" theory of inheritance. A second difficulty which flows from the same source is that Darwin had no deductive basis from which to infer the quantitative efficacy of a selective process in producing evolutionary change. Being unwilling to burden his theory beyond what the most cautious use of the analogy of man's achievements in modifying domesticated plants and animals would justify, he was undoubtedly led consistently to underrate the rapidity with which, in favourable circumstances, evolutionary changes can be brought about by natural selection.

(*b*) The objections of the second period are those which Darwin discusses at some length, as difficulties of the theory, in the sixth chapter of the *Origin*, and were evidently brought to Darwin's notice principally by scientific friends and sympathizers with whom he had discussed his theory. They are difficulties, not of natural selection in particular, but of organic evolution in general, and seem to be due to two principal causes; (i) to the misapprehension induced by earlier evolutionary speculations of the Lamarckian type, which led men to conceive of hereditary transmission as fluid and indefinite, as is well illustrated by the discussion of the difficulty "that species are well defined and not

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connected by innumerable gradations," and (ii) by the very magnitude of the conception of organic evolution itself, when considered in its entirety. The call on the imaginative faculty required to conceive of the intermediate stages, which must have connected widely diverse groups of animals and plants, must have been, and must always be, an immense one to minds not already prepared by a knowledge of the diversity and intricate adaptations of analogous forms. The elaboration and perfection of special adaptations such as the electric apparatus of fishes, or the organs of flight, or of vision, the neuter castes in insects, and the detailed appropriateness of instinctive behaviour, the design of any of which might have baffled human ingenuity, were thus felt to be objections to the theory from the very magnitude of the evolutionary vision which they revealed, although in themselves they afforded the strongest corroboration of the view that evolutionary change was caused by, or rather consisted in, the improvement of adaptations.

(*c*) The objections of the third period represent the reactions of the more conservative or recalcitrant biologists, or, for this period, perhaps one should say essayists, to the growing acceptance of Darwin's views. They introduce no new intellectual element. At their best, and when free from misapprehensions as to the nature of the theory they are attacking, they consist almost exclusively of special elaborations of "cases of special difficulty" of the kind we have referred to under (*b* ii), that is to say, of the discussion of some peculiar phenomenon, of the physiology, or the ecology, or the homologues of which little was known, and challenging the evolutionist to say how *that* was produced by natural selection. It is, perhaps, because the selectionists of this period were incidentally fighting the battle for evolution in general, that it so seldom appears to have been realized that the difficulties, such as they are, are such as must be faced by any evolutionary thinker, and are indeed far more formidable to any evolutionist who ignores the aid provided by selection theory towards their solution.

(*d*) The fourth stage was ushered in by the assumption, widely disseminated among the earlier geneticists, that the discovery of Mendel's laws of inheritance was unfavourable, or even fatal, to the theory of natural selection. To demonstrate how little basis there is for this opinion was one of the main purposes of my book. The asserted support of an experimental science did, however, for many years have the effect of reviving in the minds of critics many of the older difficulties and objections, though in a derivative and sadly degenerate condition. The logical cogency of the arguments adduced has indeed shown a progressive decadence from the first stage to the last; and, though I am unwilling to pillory otherwise excellent modern writers, it will be necessary, when we have considered the more substantial difficulties of the earlier periods, to give some examples of the manner in which they have in comparatively recent times been presented to the public.

The first difficulty discussed by Darwin in the *Origin* is that existing species are well defined and are not connected by innumerable gradations. This point should be clearly distinguished from the discontinuity of species in the geological record. The modern reader will probably have some difficulty in imagining on what suppositions the evolutionist is expected to infer that contemporary species should not be distinct. To understand how it came to be discussed as a difficulty in connection with Darwin's views, we must recognize it as an inevitable survival of the controversies engendered by evolutionary speculation of the Lamarckian type. In these, exposure to the current differences of environment, accidentally formed habits, and mental or physical exertion of any kind, were supposed to produce hereditary effects. With such a vague and fluid notion of inheritance, the evolutionist might indeed have anticipated that the variations of the existing species must spread indefinitely in all directions, and that systematic classification should be shown, as more and more material was accumulated, to be logically impossible.

The point is one that must have been pressed upon Darwin by Lyell. Indeed in his *Principles of Geology* (Volume II, Chapter I), Lyell had given a discussion of Lamarck's speculations under the remarkably illuminating heading "Whether species have a real existence in Nature," and summarizes Lamarck's argument upon the point in the words:

> The greater the abundance of natural objects assembled together, the more do we discover proofs that everything passes by insensible shades into something else; that even the more remarkable differences are evanescent, and that Nature has, for the most part, left us nothing at our disposal for establishing distinctions, save trifling and, in some respects, puerile particularities.

Since Darwin had not entirely freed himself of the Lamarckian assumption, it is not unnatural that he should have felt that there was sufficient point in the difficulty to deserve discussion, and should have discussed it with characteristic care and candour. It is probably only for this reason, though none the less remarkable, that it should have come to be considered by later writers as a difficulty opposed to the theory of natural selection.

If, in the belief that the inheritance we observe is in fact a simple process of transmission of relatively permanent elements of the germinal material, we seek for the grounds on which an evolutionist could infer a confusion of specific types, it appears that he must postulate either a completely asexual process of reproduction, or fertility and habitual mating between different species. Something approaching this latter condition does seem to exist in certain so-called polymorphic genera of plants, in which, as we might infer, classification on traditional taxonomic lines appears to be impossible. On the contrary the vast majority both of plants and animals consist of groups between which breeding is impossible or exceedingly rare, but within which there is a constant interchange of germinal material, on a scale which ensures some community of ancestry between almost every two individuals, within a period no greater than a hundred generations. With this community of ancestry in view, the reason for the possibility of systematic classification becomes readily apparent; no other consequence could be anticipated than that such classes should be divisible into distinct groups, which, when the systematicist has learnt to recognize the special criteria of each group, will seem to him easily distinguishable. A similar process of training the powers of observation is gone through with respect to quite different characters by the practical geneticist, when he learns to distinguish the effects of different individual genes. In both cases all degrees of difficulty are encountered, and the worker may need to be sustained for some time by the faith that the material he is examining really contains objective distinctions, which he may learn to recognize. The justification of this faith would seem to be, in the one case, the particulate nature of the heritable elements, and in the other the constancy of heritable differences ensured by the historical distinctness in ancestry of the intrabreeding groups.

The suggestion, sometimes stated frankly, sometimes hinted obliquely, that the Darwinian theory rendered systematic classification nugatory, or, in converse, that the success of systematic Biology is unfavourable to Darwin's views, is still alive in modern writings on Biology. It is one of the curiosities of the situation that the systematists appealed to are invariably evolutionists, although holding very diverse opinions as to the causes of evolutionary change, and that the objection which is valid against the views of Lamarck is invariably spoken of as a point against those of Darwin. Thus in 1901, alluding to the reaction of systematists to the *Origin*, Bateson thought it worth while to write:

> Should there not be something disquieting in the fact that among the workers who come most in contact with specific differences, are to be found the only men who have failed to be persuaded of the unreality of those differences?

It would, of course, have been impossible to state baldly that Darwin tried to persuade men of science of the unreality of specific differences. Darwin persuaded men of their transmutability, and it would be difficult to find a systematist to differ from him in this matter.

Such confusion is not, however, confined to professed opponents of the selection theory. In his *Short History of Biology* (1931), C. Singer (p. 548) states, with no suggestion that his views are not fully representative of modern opinion:

> Darwinian theory demanded that species should produce endless variations, some, at least, adapted to the needs of the organism. It was an essential corollary that species could not be exactly delimited. They would tend always to be giving off varieties which would gradually pass into new species. Thus the work of the systematist was merely formal, at least when regarded *sub specie aeternitatis*. The systematist, according to the Darwinian view, is not really distinguishing species from each other, but only species as they happen to exist at his particular point of time. Since new species must be ever in process of formation, we ought to be able to trace the process.

We here see one of the bases of Lamarck's theory transmuted into a corollary of Darwin's. The historian makes no similar comments on the teaching of Lamarck, who really did attack the possibility of systematic classification. He does not realize that the Darwinian view, if by this he means, as is probable, natural selection as contrasted with the Lamarckian hypothesis, implies the reality of specific distinctions, and why the recognition of real entities is "merely formal" unless the entities themselves are eternal he does not attempt to explain. The whole passage illustrates the chaos into which an originally rational discussion may fall through reliance upon thought at second-hand.

With these examples of careless and consequently confused thought before us, it is not surprising that others, whose acquaintanceship with biological ideas is more remotely derivative, should have been led into unqualified, though completely indefensible assertion. The *History of Biological Theories* by Professor Radl of Prague, commences the chapter of Species (XXVIII) with the following amazing sentences:

> Darwin's attack on the constancy of species failed. Only his most faithful disciples—Haeckel, Schleiden, Schmidt and Carpenter—accepted the suggestion that there are no species; Haeckel and Carpenter were the only workers who tried to follow up this idea practically, and in this they had no lasting success. The other Darwinists hold in theory that the word "species" does not correspond to any existing reality, but in practice they go on discovering new species, as was done in pre-Darwinian days.

As a philosopher it is surprising that Professor Radl should have confounded *inconstancy* with *non-existence*. In conjunction with this slip, which his logical training might have obviated, his stricture, that the majority of biologists, who reject the doctrines of the constancy of species, should be so incapable of rational thought as to hold in theory what is disproved by their daily practice, deserves to be put on record for its unconscious humour.

The cases of special difficulty, which were advanced in great numbers, and which were discussed by Darwin, and by his supporters and opponents at very considerable length, are all closely similar in the kind of difficulty which they present, although this difficulty may be framed in three distinguishable phases.

(*a*) An organ, such as the wing of a bat, belonging to a group somewhat widely separated from its nearest allies, may be so specialized for the particular functions to which it is adapted as to bear little resemblance to the prototype, as illustrated by the fore-limb of an insectivore, from which it must be presumed to have arisen. The difficulty felt here is that of imagining a series of organisms presenting organs of intermediate grades connecting these widely separated extremes.

(*b*) An organ of extreme perfection, such as the eye in the higher vertebrates, may show such perfect and detailed adaptation to its important function that by comparison with the obstacles which the design of such an apparatus would present to human ingenuity, the mind is staggered by the effort of conceiving it as the product of so undirected a process as trial and error.

(*c*) Some organs of seemingly trifling importance are yet so clearly adapted to the function they perform that they cannot be regarded as accidental. In these cases it may be asked how can the efficacy of this trifling function have ever been a matter of life and death to the organism, and so have determined its survival in the struggle for existence.

Of these three types of objection the first is opposed to evolutionary theory of all kinds, while the second and third, though I have stated them in the form in which they should be presented to a selectionist, can only be evaded by evolutionists of other schools by postulating a creative power in living matter equivalent to the ingenuity of a benevolent creator. They are all, in somewhat different ways, difficulties less of the reason than of the imagination. The cogency and wealth of illustration with which Darwin was able to deal with these cases was, perhaps, the largest factor in persuading biologists of the truth of his views, and would in itself to a great extent explain the enormous influence which he exerted upon biological opinion. The difficulty of imagining the intermediate stages in the evolution of the wing of a bat Darwin met by pointing to the existence in Nature, not of the intermediate stages themselves, which must necessarily be extinct, but of the analogues of a chain of intermediate adaptations, in the flying squirrels and in *Galeopithecus*, in which less specialized means for gaining assistance from the air, in leaping and gliding, indicate a series of stages, each of practical service to its possessor, without the latter enjoying the advantages of true flight. In considering such a series of stages it becomes apparent that it is the theory of evolution by continuous adaptation, amid the extraordinary diversity of the expedients which are in fact useful to different animals, which makes such transitions possible. What would be incredible in such a case would be a non-adaptive orthogenetic urge leading straight from the fore-limb of an insectivore to the wing of a bat through some thousands of generations of intermediate types encumbered with useless appendages; or, to allude to a rival absurdity, the appearance of the bat's wing by a *saltation* among a litter of primitive insectivorous mammals.

Singer, to whose *Short History of Biology* we have before alluded, repeats this particular difficulty as though it had been never mentioned by Darwin. Of "a series of fallacies and some erroneous assumptions" which he ascribes to Darwin the second is:

> (*b*) That a natural variation should confer an advantage is not enough to secure its perpetuation. The advantage must be effective and moreover it must be transmissible. Now it is difficult to believe that the earlier stages of some developments are effective. A wing, for instance, so little developed as to confer no power of flight, or at least of gliding, would be no advantage.

It might perhaps have been expected that an historian of science would use such words as "fallacy" and "assumption" in their logical senses, rather than as terms of general disparagement for opinions he disagrees with. "Assumption" is a curious word to apply to an opinion, the grounds for which occupy half a chapter in so compact a book as the *Origin*. The reader will appreciate the wildness with which the word "fallacy" is used if he attempts, as a mental exercise, to set up a logical process based on accepted observational facts, disproving the "fallacy" that the wing of a bat has been evolved through a continuous series of forms, changing at every stage, in the direction of improved adaptation to the needs of the organism.

The second type of difficulty is encountered with respect to organs of extreme perfection, of which Darwin chooses the eye as an example. Examples of this difficulty, however, if for the moment, we assume the paradox that examples of extremely minute and intricate adaptation can be regarded as difficulties of a theory, which makes adaptation the mainspring of evolutionary change—could now be easily multiplied. For not only have morphological structures showing such adaptation been described in greater detail, but the study of the regulation and development of organisms has brought to light physiological mechanisms which rival them in the perfection of their aptitude. Darwin clearly recognized in this case that the principal difficulty lay in the limitations of the imaginative faculty. In the *Origin* he writes (Chapter VI):

> Reason tells me, that if numerous gradations from a simple and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor, as is certainly the case; if further, the eye ever varies and the variations be inherited, as is likewise certainly the case; and if such variations should be useful to any animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, should not be considered as subversive of the theory.

It would be impossible to add to the cogency of this sentence, yet we may perhaps attempt to probe the difficulty more closely by examining it under the aspect of the improbability of chance variations ever conspiring to achieve what we should naturally regard as a finished triumph of design. This aspect is the better worth examining since, in the writer's opinion, it was Darwin's chief contribution, not only to Biology but to the whole of natural science, to have brought to light a process by which contingencies *a priori* improbable, are given, in the process of time, an increasing probability, until it is their non-occurrence rather than their occurrence which becomes highly improbable.

Consideration of the conditions prevailing in bisexual organisms shows that in a species without great differential fertility, and maintaining a stationary population, the chance of an organism leaving at least one offspring of his own sex has a calculable value of about $\frac{5}{8}$. Let the reader imagine that this simple condition were true of his own species, and attempt to calculate the prior probability that a hundred generations of his ancestry in the direct male line should each have left at least one son. The odds against such a contingency as it would have appeared to his hundredth ancestor (about the time of King Solomon) would require for their expression forty-four figures of the decimal notation; yet this improbable event has certainly happened. It is not easy, however, to conceive of the remoteness of the contingency as given by a number enormously great beyond our ordinary experience. In a large lottery with a million tickets the chance that a number chosen at random should gain the first prize is an almost inconceivably larger probability than that of a hundred successive males each leaving a son. To match the probability we have calculated we should need to consider the chance that seven numbers chosen at random should give the first prize-winner, the second, and so on down to the seventh, in the right order, and even then the probability of one hundred ancestors all leaving male issue would be only about a twenty-fifth as great.

This example only illustrates the difference between probabilities viewed prior and subsequent to the events they concern. Probability is, in essence, merely a statement of relative frequency. A frequent consequence of any action is a probable consequence; a rare result is an improbable one. The peculiarity of natural selection with which we are concerned is that it constantly modifies the frequency with which different types of organism come into existence, and consequently the probability of all the types of organism which might appear, whether such types are actually in existence or not. The rate at which the probability is modified will not be as great as that illustrated by the continuance of the male line, but, with selective intensities of the order of 1 per cent the lapse of 10,000 generations will suffice to bring about changes of probability of the same magnitude. And ten thousand generations is not a long period in the evolutionary history of most species.

Very large numbers are often referred to as "astronomical," and indeed astronomy has done much to stretch the human imagination in respect of magnitude of time and distance. In respect of probability ratios measuring intricacy of design, quite commonplace biological situations involve ratios as large as the largest commonly conceived by astronomers. Some astronomers believe that the universe is finite, and contains a finite number of particles (protons). This number may be illustrated as follows: A largish helping of salt contains about a gram of matter, and this would contain about a million million particles the size of a bacterium, while each bacterium contains a million million protons. A million million grams would give a sizeable hill, and ten thousand million million of these would make up the earth. Astronomically the earth appears to be a rather insignificant body. The solar system is about a million times heavier, and the sun is one of about a hundred thousand million, or perhaps four times as many, which make up the galaxy. Our galaxy seems to be a large one, as galaxies go, but there are at least two million others, and astronomers who believe that the universe is finite have made estimates of the total weight that it contains substantially larger than would be found by multiplying these figures together. The probability 10^{-79} of picking at random one particular proton out of the totality of those present in the universe may be used as a standard of comparison. A combination of characters of this order of improbability might become the prevalent condition within ten thousand generations under the action of a selective intensity of rather less than 2 per cent. Such changes have probably occurred in most living species within comparatively recent times.

That these considerations of probability are not altogether irrelevant to modern discussions may be made clear by a quotation from Professor Berg's *Nomogenesis*:

> As a case in point, what is the probability of the test in the appendicularians (free-swimming tunicates) being accidentally formed? These animals inhabit a very complicated test, which is secreted by peculiar large epithelial cells, known as

oikoplasts. In *Oikopleura albicans* the test is provided with a sieve for filtering minute organisms of the nannoplankton, an entrapping apparatus, a funnel, etc. Among the oikoplasts of this appendicularian there are two large groups—one for the secretion of the entrapping apparatus, another for the formation of the sieve (Lohmann, 1909). The test may be cast off and formed anew several times during one day, being secreted by the ectoderm. Can such a chance variation of two groups of cells be conceived, as should lead to the formation of a purposive apparatus harmonious in all its parts? If we share this point of view on probability, we are bound to say that the probability of an accidental occurrence of even one useful character in such a complicated organ as the eye, the ear or the brain is insignificantly small. A new character, accidentally produced, is very likely to *injure* a complex mechanism; to expect that it will *improve* it would be in the highest degree injudicious. But probability will very nearly approach zero, if we remember that an accidental variation of one character is insufficient for that purpose: a useful variation in the retina, for example, should be connected with variations in the whole apparatus simultaneously: not only a series of other parts of the eye, but likewise the corresponding centres in the brain should vary in the direction of usefulness. The probability that all useful variations will simultaneously occur in all the parts is the probability of a miracle. Repeating Darwin's words, it might be said, "To admit all this is, as it seems to me, to enter into the realms of a miracle, and to leave those of science. (*Origin of Species*, sixth edition, p. 204.) We might just as well expect that if the wheels, screws and other component parts of the mechanism of a watch were to be put into a vessel, we could, by the simple process of shaking, get them to combine in such a manner as to become a watch that would function as such.

It appears that this is an argument which the theory of natural selection is singularly well fitted to meet. Berg's statement of the improbability of such adaptive mechanisms as biologists have brought to light, arising by chance without selection, does not appear to be over-strained. What is strange is that he adduces it as an argument against selection theory, rather than in opposition to such theories as that of saltations, or of orthogenesis, which assume that evolutionary modification takes place by reason of causes other than the adaptive improvement of the organism. The quotation from Darwin, it may be noted, is drawn from Darwin's criticism of the saltationist theory of M. Mivart. Its citation by Berg shows how entirely in the course of time the point of an argument may become obscured.

We may now turn to the difficulty felt with respect to adaptive organs, the importance of which to the organism appears to be trifling. This difficulty has not been prominent in recent evolutionary writings, though it was taken seriously by Darwin. It is, however, valuable for the light which it throws on the logical position of argument based upon structural features, and on the difficulty of attaining to a just appreciation of the relative certainty or uncertainty of our judgements.

In the first place it should be noted that the difficulty only arises when we have already satisfied ourselves that the organ in question is in fact adapted to a specific purpose. If the adaptation itself is in question the criticism we are concerned with here cannot be developed. The selectionist is bound by no obligation to show that all characters are adaptive. Anyone, however, who rejects the alternative methods by which adaptation might conceivably have been acquired, i.e. by Lamarckism, or by the special intervention of the Creator, must be prepared to claim that all genuinely adaptive characters have become so through selection. If, therefore, it can be confidently asserted that an examination of such a structure as a giraffe's tail shows features and details which can only be interpreted upon the view that it is a protective fly-whisk, then, if this function really is unimportant in the life history of the species, it may rationally be argued that, since natural selection depends on life or death, it cannot be the means by which the organ has come to be adaptively modified to fulfil so unimportant a function.

It will be observed that the argument depends on the judgement of unimportance, and to the question of what weight can be given to such a judgement we shall be obliged to return. Its rhetorical force, however, springs from the negation that admittedly very important matters like life and death can be influenced by trifling differences, and in this aspect the argument embodies a widespread fallacy which it is of some importance to expose. It may be admitted that death and reproduction afford the final criteria by which the existence and magnitude of any injury or disability may be tested, without admitting, however, that such a test is immediately applicable in the absence of impossibly exact knowledge of every detail of the life-history and its contingencies. In cases where it is arguable whether the supposed injury really is injurious this is indeed the only test on which we could rely. If it were urged, for example, that infestation by vermin conferred the advantage of a beneficial stimulus leading to an alert and vigilant activity, sufficient to outweigh its more obvious disadvantages, the only possible final test would lie in the relative survival and reproduction of the infested compared with the uninfested animals. In practice, however, this final test cannot be applied. Still less, if we are convinced that vermin or blood-sucking flies are really injurious, can we apply it to assess the magnitude of the injury. We can only form a judgement that the injury is more or less important, and it is easy to see that the judgement that it is very unimportant compared to the death of the organism, even if this judgement is unquestioned, is an entirely inadequate basis for the assertion that it does not inflict a selective disadvantage.

The case to which the life and death test is most immediately applicable is that of capture by or escape from a predator. If we consider no outcome to such an encounter, other than escape or death, then it is manifest that the amount of difference in alertness, speed or endurance, which may decide the issue, is smaller than any assignable quantity. The difference needed to determine life or death is, in mathematical strictness, infinitesimal. For, however small the difference which we choose to consider, a finite number of increments of this magnitude will suffice, in any particular case, to determine the difference between easy capture, at the one extreme, and easy escape at the other. And some particular one of these increments, however small they may have been chosen, will therefore have sufficed to bridge the gulf between death and safety. Obviously, small advantages will make the critical difference more seldom than large ones. On our postulates, "hairbreadth" escapes may be rare, but are certainly not imaginary.

If, on the contrary, intermediate results of the encounter are to be considered, such as injury not resulting in death, a finite difference in fitness will be needed to determine the whole difference between death and complete escape; but in these cases smaller differences in fitness will determine such selective advantage as there may be in uninjured escape over escape with injury, in escape with slight injury over escape with severe injury, and in escape with severe injury over capture and death. In all cases, therefore, the disabilities from which an animal suffers will entail consequences expressible as a finite increase of the death rates or a finite decrease of the rates of reproduction. And the fact that natural selection acts by life or death, by the survival of the fittest and by the destruction of the less well fitted individuals, though it adds great rhetorical emphasis to the difficulty we are considering, does not carry us a step farther than the general recognition that all modifications that confer advantages, however slight, or which avert injuries, however apparently trivial, will be favoured by natural selection in proportion to the magnitude of their actual effects upon survival and reproduction.

We may, none the less, in so far as our judgement can be relied on, make a broad distinction between characters of great apparent importance to the life of the individual and those the apparent importance of which is much less considerable. In the case of characters of great importance, such as acuteness of vision, and of the other chief senses in the higher animals, we may infer that any appreciable differences in adaptation will be favoured by selections of a high numerical intensity, leading to a proportionately rapid genetic progress in the species. Again, in such cases, we may recognize that even small and intricate refinements of design, which add to the efficiency of the sensory apparatus, will confer a sufficient selective advantage to ensure their gradual establishment in the long course of evolutionary progress. On the other hand, with characters influencing only slightly the efficiency of the organism in its various necessary activities, evolutionary progress could only be expected to be rapid in adaptations of a relatively simple character, and especially in characters which, like human stature, are determined by an abundant supply of factorial differences. Intricate adaptations, involving a great complexity of genetic substitutions to render them efficient would only be established, or even maintained in the species, by the agency of selective forces, the intensity of which may be thought of broadly, as proportional to their complexity.

The difficulty of high adaptation of unimportant organs may therefore be genuinely felt in cases where we have substantial reasons for believing, (i) that the bionomic function is in fact unimportant, and (ii) that the adaptation is so intricate and has required so many gene-substitutions to build it up, that it could only have come into existence through the agency of selective intensities more powerful than any that our knowledge of the bionomics of the species permits us to postulate. The difficulty of adducing evidence sufficient on these two points to support a cogent argument will be obvious as soon as the form of the argument is carefully stated. A biologist who wished to satisfy himself, in the case of the giraffe, that a partial protection from the attacks of flies was, in reality, of trivial importance, would be obliged to investigate the loss of nutriment caused actually or potentially by these pests, and the frequency with which injuries to the skin due to other causes were aggravated by them. He would have to study whether the irritation and disturbance caused by their attacks harass the animals and interfere with the efficiency of their normal activities, their feeding, mating, herd reactions, vigilance, or sleep. He would have to discover whether the flies included blood-suckers merely, or insects which were internal parasites during their larval stages, whether they were the vectors of such parasites, and whether they infected the blood of their host with the germs of any distemper or disease. In the course of these investigations he would doubtless discover additional questions which required answering before an opinion could be formed as to the advantage of killing or driving away a proportion of the insects to the attacks of which the giraffe would otherwise be exposed. But the great extensions which have taken place during the last two generations in our knowledge, both of the insects and of micro-organisms, have made the considerations urged above sufficiently obvious, and almost unnecessary to the present generation. It is perhaps for this reason that modern writers have not chosen to revive this particular class of the difficulties discussed by Darwin, although it is the class which is most particularly an objection to selection theory, rather than to theories of evolution in general.

The difficulty of forming a judgement of bionomic utility is, however, only one half of the problem of comparing this utility with the magnitude of the task of bringing into existence, by a process of genetic substitution, an adaptation of an observed degree of structural complexity. Psychologically the impression of the ingenuity of an adaptation is much heightened when it is one of a kind of which we had not before suspected the existence, as though we should say, "How clever of natural selection to have thought of that!" The purely human difficulty of perceiving the need of a contrivance, or of the possibility of improving one, and of studying the situation with a view to designing its execution, is thus added to the real difficulties which the evolutionary forces have overcome, which consist only of bringing about the series of genic substitutions by which it has been in fact built up. Even when we discard these extraneous and anthropocentric elements, however, much knowledge of the common effects of genic variations, and of the developmental mechanisms by which they are brought about, is needed to form a judgement of the amount of genetic complexity to be ascribed to an observed adaptation. It has been beautifully shown by J. S. Huxley (*Problems of Relative Growth*, 1932) that relatively simple modifications in the system of growth-gradients (by which the form of organisms, both in their general structure and in that of their parts, is governed in the later stages of development) will bring about harmoniously adapted modification of form, involving numerous structural elements, and which might have appeared to require equally numerous modifications of the germinal material. The principle appears to be applicable with conspicuous success to many cases of sexual dimorphism in the Crustacea and to the polymorphic neuter castes of the social insects. It would, I believe, be an entire overstatement to deny an extreme degree of genetic complexity in the evolutionary development of some structures such as the eye. A better understanding, however, of the developmental process, may well show that conspicuous phylogenetic changes in the external form can be brought about more simply than many far less striking adaptations in detail of the organism to its environment, or of its parts to their mutual reactions.

A third point may also be considered in this connection. In cases where adequate judgements can be formed, both of the bionomic utility of an adaptive modification, and of the comparative simplicity or complexity of the genic substitutions by which it can be brought about, we shall be in a position to estimate the *relative* speed of evolutionary change. Even so, however, our data for translating this knowledge into that of absolute speed, measured in generations, or in geological epochs, is as it happens, very meagre. The hard parts surviving as fossils seldom supply a means of assessing the exactitude of adaptation to the prevailing conditions, whereas the gross changes which are observable in the size and proportion of parts are certainly in themselves the kind of modification which the very faintest selective intensities would be competent to accomplish. I do, however, suggest that an indirect basis of comparison is afforded by the modifications which have apparently taken place in the heterozygotes of certain rare, but recurrent, mutations. In those, exceptionally minute selective intensities, not easily to be accounted as more than a ten-thousandth of those at work on the evolutionary improvement of the species as a whole, have apparently sufficed to repair serious maladaptations in very numerous instances, in some of which, at least, the process of repair seems to have been completed since the separation of nearly allied species. It is not unreasonable to hope that, as this source of information becomes more fully explored, it will provide a basis of comparison for assessing the actual rates of modification possible to characters of very different kinds under the action of known selective intensities.