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ABSTRACT: The article ON THE FALSIFIABILITY OF NEO-DARWINISM, published previously in this journal, has been criticized by Mayo and Bishop. The present rejoinder tries to analyze the reason why the debate on the validity of the micromutation theory has gone on now for more than a century. Is it because defenders and opponents do not agree on terminological matters, are there logical difficulties behind the dispute, or is it possible to find another reason? In the present article it is suggested that today the most ardent defenders of neo-Darwinism are not to be found among the population geneticists, but among biologists in general, brought up within the neo-Darwinian paradigm. If this is correct, the current controversy may be interpreted in the light of Kuhn's work as the struggle between two paradigms.

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"I have a simple faith that ... semantic difficulties inspire 90% of any argument and that, when these are sorted out, both sides are doing something right" (S.J. Gould, quoted from G. Nelson, 1978, p. 324).

"if ... no discrimination between alternative hypotheses is possible, the theory becomes a vacuous exercise in formal logic that has no points of contact with the contingent world. The theory explains nothing because it explains everything. It is my contention that a good deal of the structure of evolutionary genetics comes perilously close to being of this sort" (R. Lewontin, 1974, pp 11-12).

"This situation, where scientific men rally to the defence of a doctrine they are unable to define scientifically, much less demonstrate with scientific rigour ... is abnormal and undesirable in science" (W.R. Thompson, 1958, p. XXII, my italics).

Darwin's theory of evolution, ascribing to natural selection the role as the predominant creative agent in organic evolution, was made public 120 years ago. Since then it has been acclaimed and denounced in turns, becoming the ruling theory of evolution only after the last world war, carried forward by the triumph of theoretical and experimental population genetics.

Yet, in spite of this breakthrough of the "neo-Darwinian" selection theory, the criticism has never abated; there are still a number of outspoken critics of the Darwinian selection theory and, as I have come to understand, among the biologists the number of silent opponents may be larger still. I belong to the opponents, having stated my views in three books (1974; 1977; 1979) and several articles, among which one in this journal (1976), where I discussed the falsifiability of the neo-Darwinism.

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In fact, I feel having reached the point where I have presented all possible arguments against Darwinism, few, if any, of which are my own, and for the time being I had no plans to write further on the subject. The reason for changing my mind is that Mayo and Bishop (1979) have shown me the honour to criticize the mentioned article, and that the editor has generously permitted me to defend myself.

Let me first raise the question: How is it possible that the Darwinian theories are continously exposed to criticism? This situation is surely abnormal to the extent that usually a theory constituting the ruling paradigm is generally accepted, with little or no criticism being heard.

Therefore one may suspect that there is something special about Darwinism, and it seems that an explanation may be afforded by one, or more, of the alternatives suggested by the quotations at the head of this article: (1) The standing dispute is primarily the result of careless dealing with words, (2) the issue cannot be settled because the theory is not falsifiable or (3) one or both parts do not follow the rules of the game which, in the present case, imply strict adherence to the methods of deductive logic and, of course, a frankly critical attitude towards the theory.

In the following pages I shall try to establish which of these alternatives may best account for the contribution of Mayo and Bishop.

#### Prediction and falsification

As we have learned from Popper, all our reasoning is based on theories, and these in turn are but conjecture, guesswork. To the extent that they deal with objects of the external world, the theories can be tested by confronting their predictions with empirical observations.

The elements of any theory comprise premises and, maybe, definitions, and the predictions are derived from these through reasoning, following the rules of deductive logic. In those cases where the premises can be formulated in quantitative terms, the step of deduction is facilitated, because the language of mathematics is one of logical deduction. But in all other cases the situation is much more complicated, and both acuity and criticism may be needed to avoid deception.

Nobody was more meticulous than Darwin in testing a theory against factual observation. And he was critical enough to see that the evidence afforded by Nature frequently seemed refractory to interpretation in terms of his theory. But the odds were not unfavourable, apparently, for in the latest editions of his book he had twelve chapters supporting the theory, and two chapters dealing with "difficulties" and "objections". Unfortunately, as we know now, theories can never be verified, but only falsified. Supporting evidence is therefore rather irrelevant, unless it is obtained during an attempt of falsification.

And therefore Darwin should have paid much more heed to the objections which, if resolved, would involve a really significant support of the theory. Actually, he chose to gloss over the difficulties with words, and this tradition, it seems, has survived among many of his successors.

1) Henceforth I shall refer to this paper by "M&B".

It has been postulated repeatedly, often on a slender logical basis, that neo-Darwinism is a tautology, i.e. that no falsifiable predictions can be derived from it. Mayo and Bishop consent that the state of falsifiability of neo-Darwinism is far from satisfactory. Yet, they hopefully quote some authors (Maynard Smith; 1972, Williams; 1973, King; 1975, Van Valen; 1976), who have suggested that it may be possible to falsify neo-Darwinism.

And what did these authorities arrive at? Let us begin with King, whose suggestions concern the decision between the two neo-Darwinian sects, the "classical" school and the "balance" school, Evidently, settling this issue would not imply that either alternative represents the correct theory of evolution.

To quote M&B, Van Valen "has shown that the importance of competitive natural selection for evolution can be deduced from simple premises about limitation of resources, variabilities of existing forms, inheritance of these variations, etc."(p.151). I fail to see where the question of falsification comes in, but I may add that the crucial point as regards the present issue is whether the "struggle for existence" goes on between members of the same species or of different species.

Intraspecific selection constitutes according to the neo-Darwinian micromutation theory the creative agent of evolution; in the macromutation theory, advocated by the opponents of the current creed, it is of trifling importance. On the other hand interspecific selection is the driving force of progressive evolution according to the macromutation theory, and void of interest according to its rival.

Here I think, there are indeed possibilities for testing the two theories and, as I have affirmed elsewhere, the available observations seem to support the macromutation theory.

And what are the falsifiable predictions derived by Mary Williams? Let us have a look at the first one (Williams, 1973, p.520): "Prediction I B: If  $\underline{S}$  is the set of populations of organisms existing today then  $\underline{S}$  contains populations in every recognizable stage of the transition between one species and two species".

I surely would not be very happy to test this vague statement, but fortunately it seems unnecessary: Williams mobilizes corroboration by quoting Mayr to the effect that "numerous species groups, recently analyzed throughout their area of distribution, have been found to consist of populations that represent every stage of divergence, up to recently completed speciation". (Williams, 1.c.)

What would the falsification of this prediction imply, if not Special Creation? But the issue today is not evolution or not, but the <a href="mechanism">mechanism</a> of evolution, thus, for instance, the correctness of neo-Darwinism. Is it possible that Mayo and Bishop do not understand what the discussion is all about, or do they only fail to understand Mary Williams' paper?

Like Williams, Maynard Smith (1972) is seriously concerned about the falsification problem. Let us acquaint ourselves with his views. Thus, "if ... neo-Darwinism were false one would expect to be able to demonstrate its falsity by examining the end products, that is, existing organisms. Thus it follows from neo-Darwinism that if we find an adaptively complex organ, then the organ will contribute to the survival of its possessor ... If one invents counter-examples, they seem absurd. Thus if someone discovers a deep-sea fish with varying numbers of luminous dots on its tail, the number at any one time having the property of being always a prime number, I should

regard this as rather strong evidence against neo-Darwinism. And if the dots took up in turn the exact configuration of the various heavenly constellations, I should regard it as an adequate disproof. The apparent absurdity of these examples only shows that what we know about existing organisms is consistent with neo-Darwinism. It is of course true that there are complex organs whose function is not known. But if it were not the case that most organs can readily be understood as contributions to survival or reproduction, Darwinism would never have been accepted by biologists in the first place" (l.c., p.87, my italics).

Clearly, the discussion has become ridiculous, suggesting that all other theories of evolution but neo-Darwinism imply that the various organs do not contribute to survival or reproduction. After all, every existing organism survives through reproduction.

I have now discussed all the references quoted in M&B concerning the falsifiability of the micromutation theory. And indeed, falsifiable or not, if this is the best we can do after more than a century, then surely something must be wrong with the status of Darwinism as a scientific theory.

At times attempts have been made to save neo-Darwinism by the claim that a theory of evolution concerns events of the past and that, consequently, it can not and should not make any testable predictions. Arguments of this type confound the issue. In fact, neo-Darwinism does not concern the course of evolution, this question is dealt with by phylogenetic classification. Naturally, theories of this type do not make predictions about evolution in the future, but that does not mean that they make no falsifiable predictions. However, this question is beyond the scope of the present article.

The Darwinian theories pretend to account for the mechanism of evolution, i.e. the means through which new kinds of organisms have been created during phylogenetic evolution. As I have contended in the paper criticized by Mayo and Bishop, and elsewhere, one way to test the selection theory is to see if its predictions conform with our knowledge about the mechanism through which living beings are created this very day, obtained in studies of developmental biology.

That this knowledge implies a falsification of Darwinism has been demonstrated by many opponents of Darwinism, as a reference I may mention the classical work of D'Arcy Thompson (1942).

And this is not the only way the theory can be tested. I have mentioned several others in my various publications. Some of these will be dealt with below.

## The issue

In the article criticized by Mayo and Bishop I have advocated a theory which I call the "comprehensive theory". This theory is by my critics opposed to the "synthetic theory", the currently accepted neo-Darwinian population genetical theory of evolution. This is a misrepresentation. The two theories contrasted by me are the macromutation and the micromutation theories, the latter being identical with the synthetic theory. The comprehensive theory combines these two theories, whence the name. Therefore, evidence supporting the micromutation theory does not invalidate the comprehensive theory.

Mayo and Bishop also use another terminology, contrasting at some places the "selectionist" and the "mutationist" theory. But these names are deceptive and should be avoided, for both theories imply the occurrence of mutations and of selection.

What is at stake in the present dispute is the validity of the

claim that macromutations are possible and have been of importance for phylogenetic evolution, and therefore the only logical course will be to compare the macromutation theory with the micromutation theory.

# Availability of mutations

In my article I quoted King (1972) to the effect that "there is always sufficient genetic diversity in any natural population to respond to any selection pressure". According to M&B (p.148) this statement, made by an outstanding population geneticist, "is a gross overstatement of the middle range [sic] of neo-Darwinian opinions (there are more than one, which one could hardly infer from Løvtrup's account)".

I submit that (1) every theory is nothing but an opinion, initially at least, but (2) if a whole range of opinions prevail on a particular problem, then a chaotic situation obtains and therefore (3) our main task should be to try to reject as many as possible of the alternative opinions through falsification.

As to the availability of mutations I shall suggest only two possibilities: (1) mutations of evolutionary consequence are extremely rare events, which arise at random without any reference whatsoever to needs and (2) such mutations are very common events and are therefore always available when needed.

These alternatives are extremes; the first represents the stand adopted by the macromutation theory, while the second coincides with the statement by King quoted above. I am rather surprised that this point of view represents "the middle range of neo-Darwinian opinions". What can be more available than "always" available?

Although the implications of Darwinism are not at stake here, I shall still begin the discussion with the following quotation from Sewall Wright (1967, p. 117): "The idea that evolution comes about from the interaction of a stochastic and a directed process was the essence of Darwin's theory. The stochastic process that he invoked was the occurrence of small random variations which he supposed, provided the raw material for natural selection, a process directed by the requirements of the environment and one that builds up, step by step, changes that would be inconceivably improbable at a single step".

Mayo and Bishop quote R.A. Fisher in order to specify the neo-Darwinian (selection) theory. I can understand this choice, because it is almost the only place where one can today get clear-out and unambiguous support for the selection theory. Yet, on the other hand I am surprised that Mayo and Bishop venture to use Fisher as an authority, and for two reasons. First, Grene (1960) has shown that Fisher's theory rests on a basis of conceptual confusion, hardly a secure foundation for logical thought and argument. Secondly, at occasions when I have advanced Fisher as an authority, I have seen population biologists shrugging their shoulders; apparently Fisher is not in the vogue any longer.

However this may be, Fisher has stated that his theory "is quite indifferent as to the cause of mutations, as long as they are produced somehow, with the rather minute [sic] frequency necessary to maintain a stock, or pool, of heritable variability. Given that heritable variability it can be seen, or rather, I should say it can be rigorously demonstrated, that differences in the rate of death and reproduction will produce a constant modification of the species, in

whatever directions lead to a more perfect adaptation to the circumstances in which it exists" (M&B, p.147, my italics).

All the expressions in Fisher's statement emphasized by me are worthy of contemplation, but I shall discuss only a few. First: "as long as they are produced somehow". This implies clearly that the mutations required for "constant modification" are available. A selectionist and mathematician, forced by his trade to logical thinking, cannot argue otherwise, for he knows that if the frequency of some particular gene is put to zero in his equations, then there can be no "evolutionary" change.

Thus, without variation, no selection: without selection, no evolution. This assertation is based on logic of the simplest kind, and it should be noted that the common implication of selection pressure as an evolutionary agent becomes void of sense unless the availability of the proper mutations is presumed.

I cannot help commenting on Fisher's claim that it can be "rigorously demonstrated" that a process of evolution will take place, leading to "more perfect adaption". Here we witness the confusion arising when the theoretician fails to distinguish between abstract symbols and biological reality. I believe that even today we are still missing the "rigorous demonstration" that the process imagined by Darwin and Fisher has ever taken place, at least if it is supposed to involve an evolutionary significant transformation, accomplished through the accumulation of many micromutations.

I think that these two citations concur in bringing out the four fundamental tenets common to the Darwinian theories:

- 1) Variation prevails in the form of minute individual differences.
- 2) Natural selection is intraspecific and effectuates a continous change in the pool of variation residing in a given population.
- 3) This change is directed by the requirements of the environment and results in an adaptation to the latter.
- 4) Every kind of evolutionary change can be accomplished through the accumulation of minute steps.

The basic premise of the macromutation theory and its most important consequences may be stated thus:

- 1) The major evolutionary changes are the outcome of macromutations, extremely rare events which in one step may entail a large-scale morphological, physilogical or biochemical innovation.
- 2) If the utility of the innovation is dependent upon environmental factors, it can be exploited only if it happens to arise in a proper milieu.
- 3) Innovations may confer dominance upon'a given population, permitting them to extinguish a competing organism by a process of natural selection which as a rule is interspecific. Innovations may also lead to survival through isolation as a consequence of specialization.

I think we are here facing two alternative theories, mutually exclusive. It is of course possible to accept both the micromutation and the macromutation theory, i.e. the comprehensive theory, but only the intellectually confused or dishonest can unite this standpoint with the claim of being a neo-Darwinian.

And to show how this problem is solved by a neo-Darwinian who is neither confused nor dishonest, I may now turn to Sewall Wright and quote his views on the mechanism of evolution: "Evolution after the establishment of Mendelian heredity includes two phases: (1) that within species by which there is transformation into a new species

and (2) the evolution of higher categories (genus to phylum). Population genetics applies directly only to the former since the latter does not involve crossing followed by Mendelian segregation" (1.c., p. 118).

This, I submit, is a very important statement, because it clearly implies the limited validity of neo-Darwinism as a theory of evolution, being concerned only with "microevolution". Although all the examples they mobilize in support of their position concur with view of Wright, Mayo and Bishop do not seem to realize the consequence, the limitation of the theory they defend. Or do they not agree with Wright?

Personally I think that Sewall Wright is wrong in making the distinction between two kinds of evolution, surely a satisfactory theory must be able to account for all aspects of evolution. The source of Wright's dilemma is a misapprehension of the implications of phylogenetic classification. As I have shown elsewhere (1974, 1977, 1979), once this point is cleared up, no such distinction is longer necessary, nor even possible. Yet, I agree with Wright that the micromutation theory cannot explain all features of evolution, a complement is necessary, and this is afforded by the macromutation theory.

By drawing my quotations from the leading lights of neo-Darwinism I believe I have been as fair as is possible. And it seems to me that the positions taken by these agree on the essential points, and that they conform with the interpretations I have advanced before.

# Mutation pressure

Darwin was acquainted with the existence of macromutations in domesticated plants and animals - 'sports', as he called them - spontaneous events giving rise to substantial morphological changes. In the early editions of "On the Origin" he rejected the evolutionary importance of these, fearing that they might be lost through dilution in successive generations. This was a very peculiar argument indeed, since the fact that they were known to Darwin shows that they could be preserved.

In the final edition of the book Darwin accepted the significance of macromutations, possibly under the impact of criticism from various quarters. Thus he wrote: "It appears that I formerly underrated the frequency and value of [variations which seem to us in our ignorance to arise spontaneously], as leading to permanent modifications of structure independently of natural selection" (1885, p. 421).

This position was easy to adopt for Darwin, since he was not fettered by a mathematical superstructure, the validity of which depends on the possibility of ascribing measurable frequencies to the evolutionary important variations. But for the population geneticist it becomes imperative to reject the extremely rare macromutations. Fisher was therefore logically consistent when stating the following axiom: "A considerable number of such [macro] mutations have now been observed, and these are, I believe, without exeption, either definitely pathological (most often lethal) in their effects, or with high probability to be regarded as deleterious in the wild state" (1958, p. 44).

Also here Sewall Wright takes a conciliary attitude (1964, p. 923): "Summing up, the characteristic evolutionary process may be described as the emergence of a complex of adaptions of general

significance, the rapid exploitation of this in diverse ways of life by adaptive radiations at successive lower levels, leading ultimately to gradual orthogenetic advance along each line, accompanied in some cases by extensive diversification of genera and species with jointly nonadaptive and minor adaptive aspects. On rare occasions a new, relatively general, adaptive complex may emerge at any stage in the process, initiating a new cycle. The broad course of evolution has the appearance of being guided by selective expansion and elimination among the higher categories.

This quotation contains a number of notions, italicized by me, which are elements of the macromutation theory. Thus, for instance, Wright accepts the emergence of "general, adaptive complexes at rare occasions", i.e. the basic postulate of the macromutation theory.

As concerns macromutation Mayo and Bishop refer "to the growing body of evidence ... that major evolutionary departures may be related to major changes in genome size or organization" (M&B, p.151).

So Goldschmidt was right after all in his insistence on systemic macromutations? No, for at an earlier occasion we can read: "The criticism of Goldschmidt ... and others has been adequately answered". And in this context Mayo and Bishop refer to the condescending retrospect of criticisms of natural selection by Fisher (1954). Here are discussed three objections on the morphological level. These are represented by (1) the transformation of an insectivore fore-limb into the wing of a bat, (2) the vertebrate eye and (3) the evolution of organs of trifling importance, whose contribution can hardly be a matter of life and death.

Fisher states (l.c., p. 89): "Of these three types of objection the first is opposed to evolutionary theories of all kinds, while the second and the third ... only can be evaded by evolutionists of other schools by postulating a creative power in living matter equivalent to the ingenuity of a benevolent creator".

But this is not true. The "creative power" required to construct, say, a particular vertebrate, involves the origination of the epigenetic mechanism capable of creating the animal in question. And that mechanism, and hence the creative power, must be exactly the same, whether it originates in many small-step instalments or in a few larger ones. Yet, there is a tremendous difference between these alternatives. Thus, the former implies a series of intermediate steps, which must have been grotesque in many cases. And still the theory requires that these forms have been so successful that they replaced the original ones.

In my opinion this logical deduction from the micromutation theory needs no empirial refutation, common sense suffices. The great merit of the macromutation theory is that it allows for large-scale changes in such cases, thereby avoiding the embarassment. Yet, in the opinion of Mayo and Bishop my criticisms of the "accumulation of minor variations amount to no more than the assertion that what he [Løvtrup] finds hard to accept must be wrong" (p.149). Just imagine that scientific dispute has sunk to this level:

Nevertheless, if hundreds of biologists, and others besides, during more than one century have found unacceptable this consequence of the micromutation theory, then, I believe, the fault may not lie altogether with the critics. The defenders of the theory have not endeavoured to, or at least not succeeded in, obtaining empirical evidence in support of their view. And if they do not "find hard to accept" the mechanism implied by the micromutation theory, is that

because they can imagine a solution to the problem or because they neglect it?

Do macromutations occur or not? At length Mayo and Bishop conclude that "Løvtrup's third premise, that macromutations may allow quantum jumps [my critics are careless with words, "quantum evolution" has a very particular Simpsonian meaning; I have never used this expression except with direct reference heretoj in structure and function, is only non-Darwinian to the extent that it implies preadaptation" (M&B, p.151, my italics).

Ever since the times of Aristotle one of the great puzzles to human observers of Nature is the adjustment between living organisms and their environment. To the micromutationists, Lamarck, Darwin and their followers, this phenomenon involves adaptation of the organism to the environment. It is unquestionable that the concept of "adaptation" has contributed to a lowering of the intellectual standard of biological discourse (cf. Macbeth, 1971).

Thus, much would be gained if we could part with this concept, and this, in fact, is possible if we accept the notion that living organisms arise and change phylogenetically without any reference to needs, environment and the like. From an evolutionary point of view the important point is the survival of the organisms, and in this they may succeed provided they are isolated, by chance or through specialization. It is true, of course, that many specializations permit isolation if and only if they occur in the proper environment. I suppose this is what Mayo and Bishop call "preadaption", and I fail to see what is wrong with that.

#### Extinction

"Extinction was not a problem for Darwin, nor is it a problem for many holding neo-Darwinian views" (M&B, p.148). Extinction is no problem for those who accept that natural selection ensues through interspecific competition. So was Darwin's stand and so, perhaps, is that of the neo-Darwinians mentioned above. But, should this be the case, then they are caught in a logical trap. For in the population genetical theory selection is intraspecific, and this means that the "species" can be changed through selection, but it cannot become extinguished by this means. In fact, on the premise that the variation necessary for adaptation to the environment is always prevailing, extinction should not be possible, except during catastrophies, for whatever changes take place, the organisms should always be able to follow suit.

As I have discussed elsewhere, no such predictions follow from the macromutation theory, an organism may be expected to succumb whenever it is unable to adjust to the inorganic and organic environment. In fact, the enormous extinction revealed by the fossil record is no longer a riddle, but a testimony that evolution has continuously been progressive. Mayo and Bishop write (p.148): "Extinction of a species must on occasion imply inability to adapt, so that either sufficient variability cannot have existed or the change was too rapid". So in their particular "range of neo-Darwinian opinion" extinction may occur because the variation necessary for adaptation was missing and, of course, through catastrophy.

They do not seem to realize that on this presumption evolution is directed by mutation pressure and not by selection pressure, and that the concept of "adaptation", if not that of "preadaptation", loses

its sense. Do they really think their view is representative of neo-Darwinism, at least the reasoned population genetical version?

My answer to this question is clearly negative, but to convince myself that I am not standing alone, I took to Lewontin's book, found one reference to "extinction", and read: "population genetics ... has contributed little to our understanding of speciation and nothing to our understanding of extinction" (1974, p. 12, my italics).

To Sewall Wright also extinction offers no problem. Thus he writes (1964, p. 923): "A corrollary of adaptive radiation is the extinction of outmoded types. The character of the animal and plant life of the world has been revolutionized by the extinction or near extinction of ... once dominant groups ... and the expansion of the dominant groups of today from apparently insignificant beginnings".

The phenomenon described here is clearly not the intraspecific selection which forms part of the neo-Darwinism theory, but the interspecific version envisaged by Darwin and predicted by the comprehensive theory. Wright can afford this because he does not claim universal validity for the micromutation theory, whereas Lewontin must adopt the stand that the actually recorded extinction is beyond the realm of the theory.

# Accumulation of mutations

Is it possible at all to accomplish large scale changes through selective accumulation? This question was very thoroughly discussed by Pearl (1917). This paper was written more than half a century ago, but I do not think that any more recent results can change the conclusion reached at by Pearl.

The latter first discussed numerous attempts to record selection occurring under natural conditions. His conclusion was: "in some cases natural elimination is certainly in some degree selective, while in other cases it certainly is not; and in the most favourable cases of all the selection is apparently not very rigorous" (l.c., p. 71).

Darwin was to a considerable extent inspired by observations made on domesticated animals and plants, which, he postulated, represented "artificial selection". What had Pearl, a breeder himself, to say about this? First of all, to watch our language, and especially our vocabulary. Of course, a breeder must during his work make choices as to which organisms he wants to propagate. And this choice involves a kind of selection, but it is not "selection" in the Darwinian sense. Sometimes it may mean "inbreeding". Pearl wrote (l.c., p. 97): "So fixed in the minds of most biologists not acquainted with agricultural matters at first hand is the idea that the vast majority of improved varieties of plants and animals owe their origin, or their improvement, or both, to cumulative selection of slight differences, that it appears desirable to review briefly a few of the actual facts".

And these are: "The essential factors which have been involved in the production of our best fruits, grains, vegetables, flowers, etc., have been (1) the improved conditions of domestication, (2) mutations, leading at once to new and better forms, (3) hybridization ..., and (4) the purification of previously mixed races... (1.c., p. 81, my italics).

As far as animals are concerned, the situation is less clear-cut, yet observations made by breeders of poultry show clearly that the variations distinguishing new races were never established through pertinaceous crossing of individuals exhibiting minor individuals variations; rather, the variations arose spontaneously and were established through inbreeding. And I think that a similar situation obtains, for instance, with respect to the various races of the horse.

Pearl finally discussed selection experiments, performed by experimental biologists and by practical breeders. His conclusion is rather unambigous: most of these were negative. An exception was recorded in some cases where selection was made on the basis of the genotype - i.e., the properties of the progeny - rather than on the basis of the phenotype - i.e., the properties of the parent. But this is a kind of selection which Nature can never undertake.

When Mayo and Bishop argue in favour of accumulation of mutations they quote results observed with haemoglobin and myoglobin (p.149). However, the macromutation theory does not deny the existence of amino acid exchanges in proteins accomplished by mutations. Many of these are presumably neutral or quasi-neutral, their fixation being due to random drift. Those who were not neutral may have become fixed or, even more likely, eliminated through natural selection. Thus, the macromutation theory does not reject the normalizing function of intraspecific selection. But it rejects the proposition that a protein which is not both oxygen-binding and a blood protein, can become so through a series of small-step changes, each of which involves a gradual change in one of the properties (e.g.  $26/300 \rightarrow 27/300$  blood protein) and that this change can become fixed because of its selective superiority.

Mayo and Bishop definitely do not succeed in changing the verdict of Pearl, and therefore we face the situation that all attempts to demonstrate change through accumulation of mutations have been quite fruitless, while innovation through macromutation has been observed hundreds and hundreds of times. Why deny that this phenomenon may be of evolutionary significance, why try to explain it away by some ad hoc hypothesis or another?

### Inbreeding

I wrote in my article that fixation of a mutation which occurs in a single individual "is possible only through strict inbreeding". Mayo and Bishop (p.151, my italics) observe that this statement "is based on no evidence whatsoever, but also ignore demonstrations from Fisher (1930) onward that the probability of survival of new mutations is directly dependent upon their selective advantage".

I shall make the following comments: (1) Once more, Fisher (1930) demonstrated nothing, he made some calculations; (2) the new mutation may involve "major changes in genome size or organization" (M&B, p. 151) in which case sexual isolation is likely: in cases (2) and (3) inbreeding will occur; (4) practical experience with domesticated animals and plants has shown that inbreeding is the safest and fastest way to ensure fixation of innovations.

But I grant my critics that if the new mutation does not involve isolation, then it  $\underline{\text{may}}$  be fixed through outbreeding. Yet, I am sorry to say that the  $\underline{\text{example}}$  quoted in support of their view: "polymorphisms associated with malaria" has little to do with

evolution, however useful the mutation may be. I would certainly hesitate to call it a "macromutation" or an "evolutionary innovation".

### Vulgate neo-Darwinism

The neo-Darwinian population genetical theory makes predictions about the presumptive composition of the gene pool in a given population. As long as this strict limitation is accepted, the work of the population geneticists, theoretical as well as experimental, is nothing but admirable.

But the population geneticists go one step further, and a large one too, they claim that their theory is one of evolution. This is a postulate and "an extrapolation, the boldness of which is made acceptable by the impressiveness of its basic conception" (von Bertalanffy, 1952, p. 86).

I think that sober reflection suffices to show that the boldness in this case amounts to recklessness; how can anyone seriously believe that the only biological mechanisms of importance for evolution are hereditary ones?

Yet, with the ascent of neo-Darwinism biologists of all other disciplines have faced the dilemma of rejecting a theory of evolution, acclaimed by many quarters, or interpreting their facts in agreement with the dictates of the theory. And here troubles arise: the facts are not always convincingly corroborative. The consequence has been the creation of a fraternity of epistemological equilibrists, the vulgate neo-Darwinists, whose adroitness by far exeeds the rules of the trade.

Various stratagems are employed, among which the  $\underline{ad\ hoc}\ hypothesis.$  As I showed in the paper criticized by Mayo and Bishop , Darwin was the first to use this ruse, but it has been used constantly by his zealous followers.

Another way to avoid falsification consists of underrating, ignoring or suppressing conflicting evidence. Elsewhere in this article I deal with observations on the problem of accumulation of mutations published by Pearl in 1917, observations which strongly question selection as an efficient means of evolutionary innovation. This paper is hardly ever mentioned in the literature.

If the neo-Darwinians had been able to mobilise convincing evidence in favour of their theory, the present discussion would not be waged. But without facts, how is it possible to rejoin critics? Only one means is available: words. Two ways have been followed, the first of which is to appeal to the consensus of the majority; as I showed in my previous article, this was the way Simpson answered Goldschmidt. And yet, if Simpson had known Kuhn's work he would have known that this argument carries little assurance; in fact, some recent observations suggest that Goldschmidt was right after all.

The other expedient is to answer with dogmatic postulates. As an example I shall quote some arguments raised against Marjorie Grene's discussion of two evolutionary theories (1958). Thus we may read (Bock and von Wahlert, 1963, p. 144): "Evolution is the modification of a group of interbreeding organisms". Indeed, neo-Darwinian theory can only treat changes in population of interbreeding organisms, but the corollary is that asexual organisms have not undergone evolution, which is patently untrue.

And further (l.c., p. 145): "selection being always the result of the interaction between the organism and the environment. No selection means no environment". Now, for anyone to whom evolution is more than a mere play with symbols, words and fruit flies, evolution is something going on in Nature. And, as Darwin made out, the selection occurring there is a consequence of the fact that the environment of every kind of organism tends to become sated. When this state is reached, the number of individuals cannot increase further, and whenever the number of progeny is larger than that of the parents, the exceeding number of individuals must be eliminated. To the extent this "ecological" selection is differential, selection takes place. Since this selection is much more extensive than the one observable in the Drosophila cages, it may be presumed that this phenomenon is of particular evolutionary consequence.

But it is entirely possible to imagine that certain organisms happen to find themselves, temporarily at least, in an unsated environment, and then no ecological selection occurs. As I have tried to demonstrate elsewhere, this is an essential mechanism of evolution, divergence through isolation. And this means that the correct statement would be: no selection means an unsated environment, or rather an unsated environment means no selection.

Yet, even such a simple and amply corroborated ecological situation cannot be coped with by the neo-Darwinian theory. Consequently, those who believe that this theory describes reality must ignore the latter.

And one may even go one step further and leave behind all rules of logical reasoning. The procedure is the following: empirical evidence is used to test and, when possible, falsify a theory. One can cope, logically, if not necessarily wisely, with falsifying data by means of ad hoc hypotheses. But one may also simply accept them as facts and claim that they do not refute the theory. As we have seen, macromutations are an element of the "mutation" theory, but not of the "selection" theory, but Mayo and Bishop gladly accept macromutations. Likewise, extinction should not occur, except at random (deterioration of the environment), but since we know that extinction has occurred to a large extent, this fact is accepted by Mayo and Bishop, but not of course as falsifying evidence. Neutral mutations are a very great obstacle, at least to the classical theory, but they do not bother my critics.

I believe that more examples could be found, but these suffice to show that the adherents of vulgate neo-Darwinism do not accept falsification. This happy state of affairs should be compared to the critical situation in which neo-Darwinian population geneticists find themselves today.

# Conclusion

Half a century ago Darwinism had been rejected almost unanimously by the biological community (Nordenskiöld, 1929). The rehabilitation of the micromutation-selection theory is wholly due to the founders of the theory of population genetics having succeeded in convincing those concerned that their creation is a version of Darwin's theory, hence the name neo-Darwinism.

It clearly follows that the justification of this revival depends entirely on the validity of neo-Darwinism as a theory of evolution. What do experts have to say about this question?

In his review of Lewontin's book, King (1975, p. 508) describes how the author has come to the conclusion that the controversy between the partisans of the classical and the balance theory "will never be resolved ... because the different viewpoints are less a matter of the observable facts of nature than a matter of the philosophical, sociological and political conditioning of its adherents: not a matter of what we observe, but of what we believe, which is of course, what we want to believe".

This, then, is the present status of neo-Darwinian population genetics: confronted with a multitude of empirical data, which it has taken immense efforts to procure, the scientists are still free to let completely irrelevant factors decide their lead to the "truth".

This state of affairs is, of course, bad enough, but after all it only concerns two alternative variants of the theory.

The much more serious question is whether neo-Darwinism can account for anything but changes that are trivial in an evolutionary perspective, as is claimed by the macromutation theory. This possibility cannot be excluded even today, after half a century of neo-Darwinian efforts. This is revealingly affirmed by the following statements by Lewontin (1974): "Yet it is by no means certain, even now, what proportion of all evolutionary change arises from natural selection" (l.c., p. 3) and "Population geneticists, in their enthusiasm to deal with changes in genotype frequencies that underlie evolutionary changes, have often forgotten that what are ultimately to be explained are the myriad and subtle changes in size, shape, behaviour, and interactions with other species that constitute the real stuff of evolution".

I think it is fair to state that many population geneticists today realize that they are heading towards a crisis, created not the least by empirical evidence accumulated by molecular biologists in recent years, facts which are hard to reconcile with their theory.

The vulgate neo-Darwinians are less likely to discover this situation because for their part adherence to the theory always required that they protected it from falsifying evidence. This, and this alone, can explain that the theory is defended today by Mayo and Bishop in a way that hardly any population geneticist would do.

In the introduction I presented three possible ways to explain what I would call the "survival" of the selection theory as the exclusive theory of evolution. I think the first alternative is partly responsible, we are not always sufficiently careful in our choice of terminology.

On the contrary, as I tried to show in my previous article, I do not accept that the theory is unfalsifiable, many observations are not compatible with the neo-Darwinian theory.

However, if I have succeeded in my aims, I ought to have shown that the main reason is that the majority of the Darwinians today profess the vulgate version of theory, which is not distinguished by strict adherence to the rules of logic, otherwise a precondition for all scientific activity.

As stated in the quotation at the head of my article, this situation is indeed "undesirable in science", but I do not think it is "abnormal" at all. It rather corresponds so closely to the views of Kuhn, that I think it implies a weighty corroboration of the latter.

Personally I hope that the biologists will realize this and adopt the paradigm of the comprehensive theory, which unites the

best of everything in the competing theories. Everybody would be sure to gain from such a move.

#### References

- Bertalanffy, L. von 1952. Problems of Life An Evaluation of Modern Biological Thought. Watts, London.
- Bock, W.J. and G. von Wahlert 1963. Two evolutionary theories A discussion. Brit. J. Philos. Sci. 14: 140-146.
- Darwin, C. 1885. The Origin of Species (6th ed.). John Murray, London.
- Fisher, R.A. 1954. Retrospect of the criticisms of the theory of natural selection. In Evolution as a Process (ed. J. Huxley, A.C. Hardy and E.B. Ford). George Allen & Unwin, London, pp. 84-98.
- Fisher, R.A. 1958. The Genetical Theory of Natural Selection (2nd ed.). Dover, New York.
- Grene, M. 1958. Two evolutionary theories. Brit. J. Philos. Sci. 9: 110-127, 185-193.
- Grene, M. 1960. Statistics and selection. Brit. J. Philos. Sci. 11: 25-42.
- King, J.L. 1972. The role of mutation in evolution. Proc. Sixth Berkeley, Symp. Math. Statis. Probabil. V (ed. L.M. LeCam J.Neyman and E.L. Scott) - University of California Press, Berkeley, pp. 69-100.
- King, J.L. 1975. Review of R.C. Lewontin: The Genetic Basis of Evolutionary Change. Ann. Hum. Genet. 38: 507-510.
- Lewontin, R.C. 1974. The Genetic Basis of Evolutionary Change. Columbia University Press, New York.
- Løvtrup, S. 1974. Epigenetics-A Treatise on Theoretical Biology. John Wiley, London.
- Løvtrup, S. 1976. On the falsifiability of neo-Darwinism. Evol. Theory 1: 267-283.
- Løvtrup, S. 1977. The Phylogeny of VERTEBRATA. John Wiley, London.
- Løvtrup, S. 1979. De la Vérité à l'Evolution.
- Macbeth, N. 1971. Darwin Retried An Appeal to Reason. Gambit, Boston.
- Mayo, O. and J.A. Bishop. 1979. Comments on S. Løvtrup's paper "On the falsifiability of neo-Darwinism". Evol. Theory. 4:147-155.
- Nelson, G. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. Syst. Zool. 27: 324-345.
- Nordenskiöld, E. 1929. The History of Biology. Kegan Paul, Trench, Trubner & Co., London.
- Pearl, R. 1917. The selection problem. Amer. Natur. 51: 65-91.
- Smith, J.M. 1972. On Evolution. Edinburgh University Press, Edinburgh.
- Thompson, D'A.W. 1942. On Growth and Form (2nd ed.). Cambridge University Press, Cambridge.
- Thompson, R.W. 1958. Introduction to Charles Darwin: The Origin of Species. Everyman's Library. Dent, London, pp. VII-XXIV.
- Van Valen, L. 1976. Domains, deduction, the predictive method, and Darwin. Evol. Theory 1: 231-245.
- Williams, M.B. 1973. Falsifiable predictions of evolutionary theory. Philos. Sci. 40: 518-537.
- Wright, S. 1964. Evolution, organic. Encycl. Britan. 8: 917-929.

Wright. S. 1967. Comments on the preliminary working papers of Eden and Waddington. In Mathematical Challenges to the Neo-Darwinian Interpretation of Evolution (ed. P.S. Moorhead and M.M. Kaplan). Wistar Institute Press, Philadelphia, pp. 117-120.