What is Darwinism Today?

Ernst Mayr

Harvard University

One of the dominant interests of the philosophers of science has always been the problem of theory construction. How is a new theory established? To what extent can a theory be changed? Do theories change gradually or are they replaced during revolutions?

Most of the theorizing on these questions has been done with theories of the physical sciences, but there are indications that, for several reasons, Darwin's theory of evolution does not fit in the traditional framework. For instance, the number of theories still competing with each other in the 80 year period from the Darwinian revolution (1859) to about 1940 is quite extraordinarily large, and it was not one of these competing theories that was ultimately victorious, but rather an eclectic theory in which the best components of several opposing theories were synthesized in the 1940s.

But it is not this synthesis which concerns us today but rather the question whether this synthesis was successful or whether it is indicated by the recent controversies that the synthesis has become unglued again or had never been completed.

To be able to answer this question, one must state in a few words what the opposing paradigms were that were supposed to have been synthesized in the 1930s/40s. Basically two camps were involved,

(1) the experimental-mathematical geneticists, consistently reductionist in their approach, for whom the gene was the target of selection, who studied evolution in a single gene pool, and for whom evolution was "a change of gene frequencies in populations". They did not work on problems of speciation or of the origin of diversity at higher categorical levels;

(2) the naturalists-systematists, far more holistic in their approach, for whom the individual was the target of selection, whose principal research procedure was the comparison of different populations and species, for whom evolution was a "change in adaptation and diversity", and whose major interest was the origin of organic diversity.

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Both camps agreed in the rejection of neo-Lamarckism, saltationism, and of all teleology. They also agreed in the acceptance of natural selection as the principal agent of evolutionary change. As long as there was active opposition to this alliance, they muted their disagreements, in order to display a common front. But, when finally all manifestations of the traditional opposition to Darwinism had disappeared, the hidden differences finally came again to the surface, as I will describe presently.

But there are two more general matters on which I want to comment first.

The first point is that most recent attacks on the synthetic theory by non-evolutionists were directed against the reductionist extreme of some geneticists. These criticisms are simply not applicable to such architects of the evolutionary synthesis as Huxley, Rensch, and Mayr. Furthermore, the term neo-Darwinism for the synthetic theory is wrong, because the term neo-Darwinism was coined by Romanes in 1895 as a designation of Weismann's theory. The claim by Ho and Saunders in their book Beyond Neo-Darwinism, that according to the theory of neo-Darwinism "organisms, and perforce, societies and cultures can be reduced to molecules and genes" (1984, p. 10), is a caricature of the synthetic theory.

The second point is that the claim of the collapse of the Darwinian theory and its replacement by a new paradigm is based to a considerable extent on an erroneous understanding of change in scientific theories. These critics have a rather typological concept of theories and theory formation. Laws must be universal, a single exception invalidates them. Their thinking is very much the same as that of the so-called Received View of the philosophies of Carnap, Hempel, and Nagel. Even though this positivist interpretation of theory formation is now largely rejected even for physical theories, it had never in the slightest been appropriate for evolutionary theories. Very little thought has been given up to now to the way in which theory formation proceeds in evolutionary biology. For this reason, before dealing with specific contemporary controversies and misunderstandings. I first want to comment on two particular aspects of theory formation in evolutionary biology.

(a) Theories as Opposition to Existing Theories

Contrary to most claims in the literature on the philosophy of science, new theories are rarely proposed as the direct result of induction, deduction, or whatever other method of philosophy, but rather in opposition to an existing theory. For instance Darwin's and Lamarck's theories of evolution were advanced in opposition of the theory of a constant world. Darwin's theory of gradual evolution opposed the reigning theory of supernatural design.

This reason for introducing a new theory has certain consequences. For instance, it is good strategy when one proposes a new theory to present a version that is as different as possible from the theory it is meant to replace. Once the older theory has been vanquished, it is often advantageous to modify the new theory into a more moderate version. This must be kept in mind with respect to Darwinism when one examines the role of gradualness, selection, optimization, and a populational speciation.

(b) The Gradual Improvement of a Theory

A new theory is usually very coarse-grained. Only after the opposing theory has been vanquished does the fine-grained elaboration of the theory become important. One can also compare a new theory with the map of a newly discovered continent. At first it exists only as a rough outline, with many white areas remaining to be filled in. In the case of a new theory the areas of ignorance are often referred to as "black boxes". Among examples of such black boxes in the case of Darwinism have been, and in part still are, the source of genetic variation, the exact genetic mechanism of speciation, the mechanisms producing the unity of the genotype, and the relation between genotype and epigenotype. The more complex the system is that is being explained by a theory, the more piecemeal the theory will be built up. It would be absurd to claim that an existing theory is refuted every time a black box is being replaced by a tentative or valid explanation.

1. Ambiguous Terminology

Much of the recent criticism of Darwinism is based either on the ambiguous use of certain terms or on a faulty understanding of the current Darwinian theory. There is no better way to refute these criticisms than to clarify these uncertainties and to correct the misunderstandings. This is the major objective of my presentation.

Let me begin with the difference between reduction and analysis. It is self-evident that much of explanation is contributed by analysis, that is by the study of components, such as the constituents of the whole organism (organs, tissues, cells, organelles, molecules). The study of each of these levels makes unique contributions to the understanding. The classical reductionist, however, would claim that it is the study of the lowest level that gives us the only important insight or else that one can define higher level processes only in terms of lower level constituents. Typical for the reductionist approach in evolutionary biology is the traditional definition of evolution, by geneticists, as "a change of gene frequencies in populations". The current attacks on this and other reductionist formulations in evolutionary and adaptationist interpretations are fully justified. It is not at all justified, however, to label such reductionism as either Darwinian or as characteristic of the synthesis. It is practiced primarily by many geneticists and by a rather small portion of the naturalists. Darwin himself was not at all a reductionist in this sense, since he always appreciated the importance of the organism as a whole. The shortcomings of the reductionist approach were recognized by me early in my career, as documented in my 1959 paper "Where are we?", and by Chapter 10 of my 1963 and 1970 books. Another architect of the synthesis, Th. Dobzhansky, together with his followers (Lerner, Wallace), even though a geneticist, was not nearly as reductionist in his approach as the mathematicians (Fisher, Haldane) or as Muller and his group.

Curiously, in recent years, some typologists have applied the label reductionists to those who in their analyses have descended from the level of higher taxa and of the species down to the level of the population and the individual. This is quite misleading, for analysis is not the same as reduction, and the analysis must be conducted at the appropriate hierarchical level.

2. The Multiple Aspects of Darwinism

Much of the confusion in the recent literature is due to the fact that writers did not recognize that Darwin in 1859 had proposed a whole set of theories, many of which are largely independent of each other. It will help to dispel confusion if we distinguish between these theories (Mayr 1982, pp. 505-510). Basically they fall into two groups: (a) those that simply deal with evolutionary change, particularly with adaptation, and (b) those that deal with the origin, the causation, and the meaning of organic diversity, hence particularly with common descent, the mechanisms of speciation, and with the role of speciation in macroevolution.

The problems connected with these two sets of theories are so different that they are, on the whole, studied by different groups of investigators, that is they have resulted in the development of two rather separate fields. A failure to recognize that the problems in these two fields are quite different has been at the root of some recent controversies.

Let me now take up separately some of the theories proposed by Darwin in 1859.

2.1. Evolutionary change as such.

The theory of an evolving world, first postulated by Lamarck, is now so totally accepted, indeed simply accepted as a fact, that it is no longer the source of controversies within science.

2.2. Common descent.

The theory of common descent of all organisms was nothing but a working hypothesis in Darwin's day. But by now the evidence for it is so overwhelming that it is no longer controversial except for cladistic detail. With the discovery that the genetic code is the same in all organisms, down to the prokaryotes, the descent of all existing organisms from a single origin of life is no longer questioned. Almost all taxa of organisms are monophyletic except species produced by amphiploidy, or other forms of stabilized hybridity. Another exception to monophyly are those organisms that are the product of symbiosis, like the lichens (algae and fungi), and probably the first eukaryotes. On the whole our thinking about phylogeny today is very much the same as that of Darwin. The theory of common descent is completely independent of the theory of natural selection (Mayr 1982, p. 506), as some cladists have also pointed out.

2.3. The theory of speciation (multiplication of species).

As far as speciation is concerned, that is the process by which organic diversity is produced, there has been a great deal of change and clarification since Darwin's day. The major arguments, however, are conducted within the Darwinian framework, and thus I shall say nothing further about it, particularly since there are numerous recent comprehensive treatments of this subject (White 1978, Barigozzi 1982, Echelle and Kornfield 1984). The two major current problems of speciation research are first, the nature of the genetic basis of speciation, and second, the question what percentage of speciation events is non-allopatric. These are questions that can be answered only through empirical research.

2.4. Darwin's theory of evolutionary gradualism, by contrast, remains a source of controversy. Darwin's strong opposition to essentialism and to Lyell's theory of the sudden introduction of new species forced him to promote a theory of gradual evolution. However, not only ideological reasons but also empirical ones (geographic variation, the gradual improvement of animal breeds) led to Darwin's belief in evolutionary gradualism. But what does the term gradualism really mean? In the course of the recent controversy over the validity of the theory of punctuated equilbria it became apparent that different authors had different meanings in mind. What was important for Darwin was to deny the sudden origin of a single individual that represents a new type, because for Darwin evolution was a populational phenomenon. Modern authors, however, when talking about gradual or not, very often simply think of the phenotype. It is now clear that the term gradual can suggest two different sets of alternatives: (a) the gradual change of populations in contrast to the sudden origin of founder individuals of new types (hopeful monsters), and (b) a gradual, step by step change of the phenotype in contrast to a major, discontinuous phenotypic change within a single population. The first (a) set of alternates is in conflict with Darwinism, the second set (b) is not, at least not in principle. A drastically different phenotype, if viable and if not reproductively isolated, can be incorporated in a population, leading to phenotypic polymorphism. The probability of viability and even selective superiority of drastically changed phenotypes, is very small, and it is therefore an event that probably does not very often occur in evolution. Probable cases, recorded in the recent literature, are the jaw structure of certain boid snakes and the cheek pouches of certain rodents, cases where it is difficult to conceive of a gradual phenotypic transition. Darwin, who was familiar with the ancon sheep and the turnspit dog, would presumably have accepted such cases, even though after his encounter with Fleeming Jenkin he was even more reluctant to accept the evolutionary significance of discontinuous morphological changes than before. However, to repeat, such changes are not, in principle, non-Darwinian.

2.5. Natural selection.

Among all of Darwin's evolutionary theories none faced as much resistance as his theory of natural selection (Mayr 1982). For 80 years after the publication of the Origin it was accepted by only a minority of biologists. Even today almost all the objections that are raised against Darwinism are directed against one or the other aspect of the theory of natural selection. It is only within the last 20 or 30 years that the nature of the difficulties was fully understood. Several authors, particularly Tuomi (1981), have pointed out that natural selection is not a specific theory but a very basic general principle, which as such can neither be refuted nor does it have predictive powers. It becomes a specific theory only when enriched with specific ancillary assumptions, for instance with the theory of particulate inheritance, the postulate of small mutations, and the occurrence of genetic recombination. The principle of natural selection can also be formulated in a theory based in part on soft inheritance, as was Darwin's original theory. This proves the independence of the principle of natural selection of particular ancillary assumptions.

The claim that the theory of natural selection is tautological has been refuted so many times that it is not worth going over the argument again. Lewontin (1970), Brandon (1981), and others have presented clearly non-tautological formulations of the theory. Darwin himself had already singled out the essential components of the theory. The first is that in every generation there is a great over-production of individuals, only a small percentage of whom can survive and reproduce. Secondly, all these individuals have different phenotypes which, at least in principle, differ in their adaptedness to their common environment. And third, the causes of the differences in adaptedness are in part heritable.

It follows, by simple logic, that those with the highest adaptedness have the greatest chance to survive and to reproduce, and that this, in due time, will lead to a change in the properties of the population.

Most objections to natural selection are based on a whole series of misconceptions, some of which I shall now discuss.

The most important is the failure to see that _natural selection is a two-step process_. -- Even though Darwin made it clear that natural selection was a two-step process, the first consisting of the production of heritable variation and the second of the testing of this variation (Mayr 1962), this dual nature of selection was almost consistently ignored by the opponents of Darwinism, who never tired of asking, "How can natural selection make something new when all it does is to eliminate the unfit?" Virtually the same question was asked by some recent critics who thereby revealed an appalling ignorance of the process of selection. When an author asks, Is evolution due to molecular processes or due to selection?, it amounts to asking: "Is evolution a change due to step one or step two of natural selection?" Actually the two steps are completely inseparable and the question thus is quite meaningless. As the second step in this process, selection _sensu stricto_ is an _a posteriori_ process dealing with the previously produced variation and not a process which itself produces variation.

Let us begin with a discussion of the first step, the production of variation. Darwin knew virtually nothing about this and most of his ideas on the subject turned out to be erroneous. Exactly how variation is produced is quite irrelevant for the theory of natural selection, some of it could even be Lamarckian, provided that it is heritable and that it is able to affect the adaptedness of the phenotype. Curiously, many critics of natural selection omit this first step altogether, assuming that natural selection, in a teleological manner, makes its own variation.

For the Mendelians, mutation was the driving force of evolution.

However, the formula 'evolution is due to mutation and selection' remained popular among certain geneticists even after the saltationist ideas of Bateson and De Vries had been discarded. This simplified formula became obsolete as the result of the evolutionary synthesis. This was due to two insights: (1) that it is recombination rather than mutation which provides the actual material on which selection works, and (2) that whole individuals (the product of recombination) are the target of selection, rather than single genes. When current critics attribute to the Darwinians the view "that all or almost all of evolution can be explained by natural selection of random mutations" (Ho and Saunders 1984, p. 11), they are reviving an explanation that as far as most Darwinians are concerned has been obsolete for more than 40 years. The fact that it is recombination rather than mutation which is directly responsible for genetic variation, accounts for two aspects of natural selection. First the abundance of different phenotypes (based on different genotypes) available for selection, and second, the creativeness of natural selection, which is due to the unpredictability of the properties of individuals produced by recombination. It needs emphasizing that recombination can create something truly new, something that had never existed before.

Darwin's theory was a complete break with pre-existing thinking in several ways. First, it rejected essentialism, according to which all individuals are manifestations of the same unchanging underlying type. Secondly it replaced, so to speak, the hand of God by the hand of Nature. And thirdly it replaced the widely accepted principle of elimination (the removal of the unfit) by the principle of selection (the favoring of the best adapted) (Mayr 1982, pp. 488-490). A principle of elimination, that is a removal of inferior individuals ("degenerations of the type") was widely accepted by essentialists. Rather interestingly, even after 1859, the point was raised frequently that an elimination of misfits could not result in evolutionary advance. These critics failed to see that Darwin's theory was fundamentally different from the old elimination theory of the essentialists. Elimination is, of course, still recognized by the evolutionist as so-called stabilizing selection. Such selection is particularly active during ontogeny. What certain authors have referred to as internal selection is, for the most part, such a removal of defective zygotes (Remane 1983).

3. Target of Selection

For the sake of computational convenience, and also guided by their reductionist philosophy, the mathematical geneticists opted for the gene as the target of selection or, as it is sometimes misleadingly called, the unit of selection. By contrast the naturalists, from Darwin on, have insisted that it is the individual as a whole that is the target of selection. This choice would seem to be valid for several reasons. First of all, it is the individual as a whole which either survives or does not, which either has or does not have reproductive success. Furthermore, a given gene may vary greatly in its selective value depending on the genotypic background on which it is placed. This view, which I have vigorously promoted for a long time (Mayr 1963) is now also admitted by philosophers and geneticists (Sober and Lewontin 1982).

This case is an instructive illustration for the frequent situation where analysis should be pursued downward only to the appropriate level and not to the lowest of all possible levels, as some reductionists recommend. Darwin clearly thought not only of particular aspects of the phenotype but of the organism as a whole, as indicated by his reference to "the whole machinery of life" (1859, pp. 83, 85-86). Darwin's language clearly refutes the view of some authors who consider as phenotype only that which is visible from the outside. Actually any product of the translation of the DNA blueprint is part of the phenotype (Mayr 1983, pp. 48-49). This is one of the reasons why one cannot make a distinction between internal and external selection. Some recent discoveries of molecular biology (transposons, molecular drive) have been cited as a special kind of molecular selection in conflict with individual selection. If such processes should have an influence on the course of evolution, as is possible, this alone would not qualify for the designation selection, for they simply represent biased variation. Furthermore, as soon as they affect the properties of an individual, they will be subject to ordinary natural selection.

The insistence that the individual as a whole is the target of selection, rather than separate genes, would be unimportant if the genotype were an aggregate of separate, independent genes. However, there is an opposing viewpoint which considers the genotype as a well-integrated system analogous to an organism with structure and organs. This viewpoint is forcefully presented in Lerner's (1954) Genetic Homeostasis and in my own writings (1963, 1975). The controversy between this viewpoint and the reductionist one, both within the Darwinian framework, has not yet been resolved. There is, however, a great deal of recent evidence that the system of interactions among components of the genotype is far more complex than conceived of in classical population genetics. The system nature of the genotype is strongly corroborated by the recent recognition of the great functional diversity of kinds of DNA. Much of the recent criticism of "neo-Darwinism" is directed against the strictly reductionist conception of the genotype. These critics do not mention that other representatives of the synthetic theory, like Waddington, Rensch, Mayr, Lerner, and members of Dobzhansky's school have for many decades adhered to a far more holistic concept of the genotype.

Accepting the individual as a whole, rather than the gene, as the target of selection largely resolves the problem of so-called neutral evolution. When the enormous extent of the variability of enzyme genes was discovered in the 1960s, Kimura and other authors advanced a neutral or 'non-Darwinian' theory of evolution. According to this theory, most of the variation of the DNA within and between species is due to the random fixation of nearly neutral alleles by genetic drift. Kimura (1983) still upholds this theory, but a more moderate version of the theory is now generally adopted. It seems to be true that some genetic variation is indeed "neutral" but a great deal of research, some of it summarized by Ayala (1974), has shown that a selective value of much of the supposedly neutral variation can be demonstrated when the proper tests are made. What is particularly misleading is the claim that neutral variation is "non-Darwinian". Such variation relates to the first step in natural selection, and with the individual as a whole the target of selection, it is not surprising that numerous nearly neutral and some even mildly deleterious genes are carried along as "hitchhikers" of favored genotypes. The claim by Ho and Saunders (1984, p. 4) "that the majority of genetic variations are of no physiological or phenotypic consequence" is not at all substantiated in spite of Kimura's similar claims (see Gillespie 1984, p. 732).

I shall not, for lack of time, discuss the question whether or not group selection and species selection exist, except for saying that the possible existence of such processes would not be in conflict with the Darwinian theory of natural selection.

Nor does time permit me to discuss aspects of macroevolution, in particular the relation between micro- and macroevolution. There has been much clarification in recent decades -- also much controversy, as must be admitted, but none of the new insights is in conflict with the Darwinian theory.

4. Summary

I can best summarize my comments on the question: "What is Darwinism today?" by answering three questions:

(A) First: Have the discoveries of the last 50 years, and particularly those of the last 15 years, refuted Darwinism or at least some major thesis of it?

My own answer to this question is a resounding "No!" as is the inevitable conclusion emerging from the preceding analysis of the major current controversies in evolutionary biology.

(B) The second question is: In what respects does the modern theory of Darwinism differ from Darwin's own version? Here we can provide a substantial list of differences.

(1) We make a far clearer distinction between the first step of selection, the production of genetic variation, and the second step, the actual selection.

(2) Darwin had no knowledge of the origin and the nature of genetic variation. Indeed, he even accepted a certain amount of inheritance of acquired characters. We now benefit from 85 years of genetic research, and particularly from the insight that proteins cannot convey information back to the nucleic acids.

(3) We now have a much better appreciation of the great role of chance in evolution, particularly in the production of genetic variability.

(4) We now have a much better understanding of the populational nature of evolutionary change, which, in turn, explains why evolution by necessity must be gradual in spite of the discontinuous nature of the genetic material and sometimes even of phenotypes.

(5) We have a much better understanding of the process of speciation, and believe that allopatric speciation is the prevailing process, particularly in peripherally isolated founder populations.

(6) We understand even better than Darwin that there is great variation in the rate of evolution, and, in particular that many species, perhaps even the majority of them, experience long periods of stasis.

(C) My third and final question is: Where are still the greatest gaps in our understanding of evolution?

There is no doubt in my mind that it is our very incomplete understanding of the molecular structure of the genotype and its functioning during development.

The exploration of the structure of the genotype will be the great frontier of evolutionary biology in the coming decades.

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