EVOLUTION OF THE EVOLUTION THEORY

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The discovery of the specificity of living things expressed in the particular modes of their conservation and modification, is a recent phenomenon.

One can find in the ancient writings many testimonies of a conception of the origin of life in which the distinction between minerals and living things is not clearly made. In his Timaeus, Plato showes men uprising from the earth, and this point of view is also present in the celebrated : "Dust thou art, and unto dust shalt thou return" (Genesis 3, 19). We have to wait until Pasteur to see it definitively eliminated.

This passage from a form to another is not conceived as obeying laws. The Metamorphoses of Ovid show Attys transformed into a pinetree or Io into a cow. Sure, people know that, in the ordinary way of life, animals and plants produce a progeny similar to themselves, but this does not appear as a internal ineluctable necessity. Fairies, devils and gods can decide otherwise.

To comfort Cinderella, a fairy can transform a pumpkin into a coach or rats into horses and, at the very time of Perrault, one speaks still seriously of a woman of Freiburg giving birth to a living goose.

It is a paradox that, for a specific theory of evolution to become possible, thought should go through a period where every possibility of change, unless minimal, is excluded from the universe of forms. The theory of the fixity of species, to which the names of Ray and Linneaus are attached, is the discovery of the distinction. This affirmation of absolute permanence, with all its unilaterality, conveys a reality : the impossibility to pass arbitrarily from one form to another.

But, as forms change, as there is a way from one form to another following determinate laws, the turning of permanence into an absolute, characterising the theory of the fixity of species, cannot escape contradiction with the observation of reality. That is why the transformist conception of the passage from one form to another, according to laws, came into existence. Here one can evoke such names as Maupertuis, Buffon, the German philosophers of nature and Goethe.

It is to Lamarck that we owe the elaboration of a complete theory of evolution based on irritability, feeling, will, hereditary influence of needs and habits, usage and non-usage, in chanching circumstances of environment. Sure, the Lamarckian point of view appears astonishingly primitive to our modern eyes, but before judging it, we should not forget that biology was still in its infancy. At the time, the cellular structure had not yet been recognized as the basic pattern of the organisation of the living world, organic chemistry was still toddling, and yet Lamarck boldly asserted the unity of the living world, including man, and its evolution according to natural laws. It was a fact of tremendous importance. Some time later, Darwin paid tribute to his predecessor by saying that Lamarck had done a big service in declaring that every change in the organic, as well in the inorganic world, was the result of a law and not of some miraculous intervention.

Nevertheless, there is a world between the Darwinian and the Lamarckian conceptions of evolution. They are separated by half a century during which biology lived and grew vigorously. I would like to characterise rapidly Darwin's contribution, because of its important influence on modern biology. First, Darwin presents a huge documentation on the real facts of the transformation of species. His documentation is essentially historical, calling to paleontology, geographic distribution of forms, embryology, comparative anatomy. So, evolution is conceived as a single and irreversible process.

But early, Darwin feels that this documentation, abundant as it is, is not enough to gain his colleagues' approval, as he can see in his discussions with the geologist Lyell or the botanist Henslow, and as shows the history of ideas itself, because after all, Darwin is not the first to produce this kind of testimonies, even if a work of many years allowed him to collect so many evolutionary facts, far more that any of his predecessors.

He felt necessary to put forward a theory accounting for the tural character of the process of evolution. He finds the root of this theory in the work of animal and plant breeders, the kind of practical men for whom the possibility of transformation of forms is not a theoretical problem, but the very aim of their activity. This artificial transformation realised in practice, Darwin generalises it to the whole of nature in the principle of natural selection.

It is interesting to note that, in the Origin, Darwin makes a distinction between principles and laws. He calls principle of heredity the universal recognizing of the likeness of parents and progeny, and principle of selection, the cumulative choice of variants in the aim of transformation, used in the formation of domestic races.

At the same time, Darwin shares the complete ignorance of the time on the laws of variation and heredity, adopting himself very old theories of heredity. Principles so appear as generalisations at the phenomenal level, whereas laws, the product of scientific activity, are going to the essence.

If heredity, the specific form of the permanence of living things, and variation, the specific form of their change, obey unknown laws, it is sufficient that these laws exist : then, natural selection, acting as a cumulative filter of variants, gives movement to adaptation and coadaptation of forms. Several times, Darwin insists on the necessity for biologists to explain adaptations. The bill of the woodpecker, adapted to the extraction of insects under the bark, the seed of mistletoe, transported by birds, appear as the present term of a process, the nature of which must be explained.

Darwin's was a pioneer's work, but giving the lines of a research program still largely inspiring biologists.

This shifting of the centre of gravity of the conception of living things is well brought out by ewontin : for Darwin, evolution was conversion of variation between individuals within an interfertile group in variation among groups in space and time. Such a theory takes necessarily the variation between individuals as the essence. The importance thus given to variation gives Darwin's works their so pronounced historical bent.

In the years following 1859, comparative anatomy quickly becomes the most influential biological science and certainly contributes to the main bulk of "proofs", leading to the general acceptance of the theory. Carl Gegenbauer can be considered as the characteristic scientist of the morphological research of that time, where the study of the structures of the animal body has their history as end. This historical approach, often symbolized by phylogenetical trees, was to be upset by the discovery of the laws of heredity.

One of the most important contributions of Mendel to the general conception of evolution is the distinction between genotype and phenotype, that is between the intracellular elements determining the particular specificity of living things, the genes, and the manifestation of characters in individuals living in determined conditions of environment. Characters are the result of interactions between genes and environment, acting in the development and life of individuals. Genes, and not characters, are transmitted by gametes, the only material link between successive generations in sexually reproducing species. Particular genes, in different conditions of environment, will determine different characters. Different genes, in given environmental conditions, will determine identical characters. That is why the mere observation of phenotypes does not allow the prediction of the future in the selection. A selection will modify progeny, only if phenotypical differences correspond to differences in the genetical structure.

While the Darwinian thought worked at the phenotypical level, genetics goes inside the cell for determining structural differences. Its peculiar tool, the statistical analysis of progenies, that is of familial relations, has however a limit. It is not possible to go outside the species, because the possibility of crossings is the condition of the detection of genotypical differences. That is why genetics concentrated, at that time, on evolution inside populations, showing the consequences of mendelian laws of genic transmission, on the genetic composition of populations. Conservation laws through generations are then put in evidence.

A second important aspect of classical genes, sometimes called atoms of heredity, is the recognition of the fact that they were individualy distinct. The discrete character of the genetic material allows a constant renewal of combinations of genes, in the stochastic process of production of gametes, and even in the stochastic process of cellular division, owing to somatic crossing-over. This possibility of diversification is at the cost of the stability of the adapted type in constant conditions.

The discrete character of the genetic material explains a well-known and difficult problem in Darwin's times : the keeping of variability in population in time. In the old hippocratic theory of the "mixture of bloods", still accepted by Darwin, we expect a progressive homogeneisation of populations, and in particular, we expect to see the progeny of exceptional individuals regress rapidly to mediocrity. How then explain the cumulative character of natural selection ? To do it, Darwin was compelled to admit the production, at every generation, of a huge quantity of variants, a production for which proofs were lacking. It was a difficulty for his theory. We know now that genes are not mixed, they exist in juxtaposition in normal cells and can separate to go through the gametes.

In the first half of our century, what about the problem of the change of biological structures ? The distinction between genotype and phenotype shows that biological change splits in genetical and non-genetical change. But from this, it does not follow that we have absolutely to separate the effect of genes and of environment on characters. Genetical change is always expressed in determined conditions of environment, non-genetic change is always the change of a living thing, and then the non-genetic change of a genetic structure.

But if genetical structures alone are transmitted to progeny, the relevant change for evolution is the change of the genes. A particular gene is subject, with low probability, to chemical changes called mutations. Genes being associated in more complex units, the chromosomes, are also likely to be reorganised. The advantage or disadvantage of a mutation depends on the interactions and is not a property of the genes. In classical genetics, genes are conceived as elementary units, and a mutation appears as a change of state of the genes, the differents permitted states for a particular gene being called alleles. Mutation, as a recurrent process, takes the gene a random walk on the allelic states, in finite number. We know now that this cyclic change is mainly determined by the errors of replication appearing in the process of cell division. So the cycle of forms loses its historical character and particularly its irreversibility.

It is quite interesting to see how, in the models of evolution of population genetics, time is reduced to the abstract form of classical mechanics. The immense wealth of forms, of transformations, of gains and losses of functions and organs completely disappears from the evolutive interpretation. We only hear of measuring rates of mutation, intensities of selection, adaptive values, consanguinity rates and population effective sizes. It is the price we pay to know laws.

In order to illustrate this complete modification of the point of view, we can consider the concept of adaptive landscape, that is the geography of the surface of adaptive value of a population plotted against gene frequencies. Such are now the peaks and valleys where theoretical geneticists walk. To be sure, the knowledge of the laws of heredity gives the darwinian selection theory a new and impressive basis. But, as already noted, the limit of crossings, and the resulting impossibility of comparing distant groups, is a weakness underlined by opponents saying that genetics explains micro- but not macroevolution. In the opposite direction, the same limit has the consequence of some discredit, in the new biology, put on the so-called "descriptive" sciences, as embryology and comparative anatomy, the old queens of the preceding period.

In the fifties, the builders of the new theory of evolution, sometimes called *synthetic theory*, or *neo-Darwinian theory*, highly conscious of the vigor and originality of their effort, show a tendency to consider the theory of evolution as practically complete. Due allowance being made, this period is not without similarity with Lord Kelvin's time, when physics was believed to be almost complete. The general explanation by way of mutation and natural selection sometimes takes a scholastic flavour, with its capacity to explain, in words, all facts of evolution by this simple rhetoric. These certitudes were to give way to molecular biology. Its discoveries convert the gene from an atomic particle to a long molecule of DNA, high polymer of nucleotides. Each nucleotide has three parts : a puric or pyrimidic base, a sugar, a phosphate. A gene is characterised by the sequence of the bases in the polymer and the genetic code gives the rules by which the sequence of bases determines the sequence of aminoacids in the protein resulting of the activity of the gene. The difference between two alleles is no more a global difference of states, but a difference between some bases in two homologous sequences.

As an example, let us consider haemoglobin. This protein is formed of four aminoacid chains, homologous two by two : two α chains (141 residues each) and two β chains (146 residues each), each chain being associated with a porphyrin, the haeme. We know the complete sequence of aminoacids of the chains in normal human haemoglobin, and also in many abnormal haemoglobins. So, haemoglobin S, giving the sickle-cell anaemia, differs from the normal A haemoglobin by only one aminoacid residue of the chain, a glutamine being substituted by a valine. This localized alteration is linked to a particular mutation of the gene coding for β chains, that is a modification of the base sequence in the DNA molecule.

The considerable growth of molecular biology in the sixties has given us more and more sequences of proteins, and progressively sequences of DNAs themselves. The Atlas of proteins sequences published by Eck and Dayhoff became the bible of evolutionists, evolution being thus taken at the elementary level.

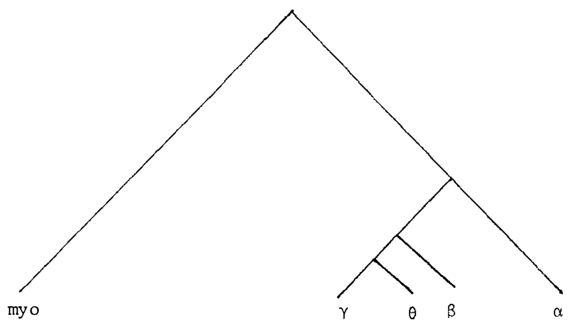
Let us come back to human haemoglobins. We know of six types of chains, α, β, γ, θ, ε, τ. The last two, being foetal haemoglobins are less studied. We observe great similitudes between sequences of α, β, γ and θ chains, more than one third of aminoacid positions being identical. We can think that the four chains have been produced by genes, first duplicated and, after duplication, evolved separately by mutation.

Differences are presented in the table, together with myoglobin.

	myo	α	β	γ
α	119			
β	118	89		
γ	118	84	39	
θ	117	85	41	10

This shows well the degree of divergence of forms, and allows some hypotheses on the history of human genes for globins.

A tree likes the following one gives a representation.



We know too sequences of haemoglobins for other species. The α chain of man and horse differ in 18 positions. The two chains are then more similar than human α and β chains. We can conclude that the duplication of α and β chains occured in the ancestor of man and horse, a long time before their divergence of the two species. We see that molecular genetics gives us the possibility to go through the barrier of crosses. We can now compare distant species and groups. Even plant globins can be compared with haemoglobins.

In these comparisons, we are at a level different from anatomic evolution. But, after the period of conceptual austerity of the synthetic theory, the evolutionist finds again in the molecules all the variety of the living world and can rejoice in their morphogenesis and comparative anatomy. Again, history wins the game. But laws are still waiting in the shadow. And the most warranted certitudes of the synthetic theory are now contested.

Kimura, measuring rates of evolution in haemoglobins for different lines, finds them nearly constant. From the great variety of environmental conditions through which lamprey, carp, horse or man found their way, he deduces that natural selection has <u>no effect</u> on the diversification of molecular forms : this is the <u>neutralist</u> theory, comforted by others like King and Jukes. They give to this the blasphematory name of <u>non-darwinian evolution</u>. Kimura extends these assumptions to the huge polymorphism found in populations for enzymes, not without fierce oppositions.

A new abstract space comes to birth, the space of sequences, with its ten to the nine or ten to the twelve dimensions, where theorists prepare themselves to dream, and will may be find some Thom's catastrophes.

But more important, new evolutionary problems come on the stage : of the genetic code ; experiments of acquisitive evolution ; origin and progressive augmentation of the reliability of replication and translation, condition of the complexification of organisms ; origin of life ; and so on.

The balance between history and law, structure and function continues to give matter to experiments and controversies, conducting biology in the ways where physics preceded it. Less than the relative importance of neutral and selective evolution, the question is now the actual ways of these modes. Darwin is outdated by the exploration of the very territories he opened and is, in this way, truly justified.