How Theodosius Dobzhansky integrated genetics with evolution

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In 1859, Charles Darwin proposed his theory of natural selection which acts on variations present in the populations and better varieties are produced in the course of time. Darwin's theory of natural selection is important, and acts as the main guiding force of evolution. However, he lacked the knowledge of genetics and could not explain the basis of variations. It is only those variations which are important in evolution that have a genetic basis and are inheritable. This gap was filled by Theodosius Dobzhansky who provided the genetic basis of evolution through his book in which he explained various mechanisms of evolution having genetic basis. Dobzhansky also provided the experimental evidence in favour of evolution through his work on Drosophila. He was the first to provide the genetic basis of evolution showing the action of natural selection on genetic variability. He defined evolution as a change in genetic composition of a population. Further, he also contributed to the development of the modern synthetic theory of evolution. That is why the author says Dobzhansky integrated genetics with evolution.

Keywords: Evolution, genetics, modern synthetic theory, natural selection, population variations.

IN 1744, the German biologist Albrecht von Haller was the first to use the term 'evolution' based on the Latin verb 'evolvere' for the noun 'evolutio', which means unfolding or unrolling[1,2]. However, he used the term to describe the theory of progressive unfolding of structures during embryological development. Haller's embryological evolution was transformed into different meaning when Charles Darwin proposed 'descent with modification'. Darwin did not use the term 'evolution'; rather he used the term 'evolved' in his book *On the Origin of Species by Means of Natural Selection*[3] published in 1859. In the 19th century, the term 'evolution' became more popular because of Herbert Spencer[4] in England, although he was not a biologist. He was called the 'Father of social Darwinism'. To some extent Spencer believed in both Lamarckism and Darwinism, although his influence declined in the last part of the 19th century.

Though the idea of evolution is usually associated with Charles Darwin, it appeared even in the ancient Greek writings (600 BC); but the idea was vague and unacceptable. For a certain period of time it was thought that the world is a special creation of God and is unchangeable. For many centuries the idea of evolution remained unchanged. Interestingly, Aristotle (384–322 BC), who was a philosopher and biologist, put forth the idea that organisms are arranged in the order of increasing complexity (ladder of life), which was really meaningful indicating the evolutionary change from simple to more complex. However, the idea of evolution was revived in the medieval period by evolutionists like Bacon, Bonnet, Kent, Oken and others. The contribution of Linnaeus, Buffon, and Erasmus Darwin was also important in shaping the idea of evolution. Erasmus Darwin, grandfather of Charles Darwin was also responsible for giving shape to the idea of evolution of his grandson.

As far as modern biology is concerned, the French naturalist Jean Baptiste Lamarck was first to recognize and demonstrate the facts of evolution. He proposed a theory to explain the mechanism of evolution in his book *Philosophie Zoologique* (1809). He realized that all life is product of evolutionary change. The theory which Lamarck proposed is known as 'Inheritance of acquired characters'. It is also known as the theory of use and disuse, but evolution cannot take place because of use and disuse of organs. This theory was severely criticized and not accepted. Now it is of historical importance.

The theory of evolution was proposed by Charles Darwin from England, who travelled extensively and made several observations. This was published in a book and has two components: (i) descent with modifications – all species living and extinct descended from one or few original forms of pre-existing species, and (ii) natural selection is a causative agent of evolutionary change. His theory is primarily based on two observations and two basic conclusions.

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Observations: (i) All organisms exhibit variability, and (ii) large number of progeny is produced and there is prodigality in nature. The number produced is more than can survive because of limited food and shelter.

Conclusions: (i) The environment selects out (natural selection) those individuals best fitted to survive while those which are less fitted fail to reproduce, and (ii) the characteristics thus favoured by natural selection are passed on to the succeeding generations. The theory of evolution proposed by Darwin was acceptable to a large number of evolutionists and biologists. Even today his idea of natural selection as a causative force of evolution is important. According to Darwin, as many more individuals of each species are produced which can possibly survive, this leads to frequently occurring struggle for existence between individual organisms. Thus the total environment, including all kinetic forces caused by physical and biotic factors, acts as a selective force sorting out those variants best adapted to the particular environmental conditions and eliminating those individuals who are less fitted for survival in the same environment. However, Darwin's original concept of natural selection was unsophisticated and it was applicable to individuals rather than a group of individuals constituting a population; but certainly his recognition of this basic principle of natural selection was important and provided the basis for understanding the mechanism of evolution through this process. Darwin could recognize the extensive variability in populations of different species. However, the greatest drawback of his theory was his lack of knowledge of genetics. Mendel's laws of inheritance were proposed in 1865–66. So Darwin was not aware of Mendelian genetics. All variations are not inheritable; only those which have a genetic basis are inheritable and important for evolution because genetic variability generated by mutations and recombination provides raw materials on which natural selection operates. The missing link in Darwin's argument was provided by Mendelian genetics. The rediscovery of Mendel's laws in 1900 laid emphasis on the role of heredity in evolution.

Theodosius Dobzhansky: integrated genetics and evolution

Theodosius Dobzhansky, a Russian geneticist who moved to USA did extensive work on population genetics of *Drosophila pseudoobscura*, *Drosophila persimilis*, *Drosophila willistoni* and others. He showed for the first time in 1947 that inversion polymorphism in *Drosophila* is adaptive and subject to natural selection in 1947 (see ref. 5). His work on inversion polymorphism in natural and laboratory populations of *Drosophila* clearly demonstrated the role of natural selection acting on genetic variability. Thus his work provided support to the natural selection theory of Darwin. Hence Dobzhansky is also known as Darwin of the 20th century[6]. In 1937, Dobzhansky[7] wrote a book entitled *Genetics and the Origin of Species*. It advanced a comprehensive account of the evolutionary process in genetic terms laced with experimental evidence supporting the theoretical arguments. It had an enormous impact on experimental biologists, evolutionists and naturalists, who rapidly embraced the new understanding of the evolutionary process as one of the genetic changes in populations. Evolution is defined as a change in genetic composition of a population. Dobzhansky emphasized different topics in his book related to the genetic basis of evolution such as mutations in populations, selection, adaptive polymorphism, race formation, isolating mechanisms, species as a natural unit, population as a unit of evolution, balanced polymorphism and heterosis, genetic coadaptation, Hardy–Weinberg law, hybrid sterility, etc. Dobzhansky added the genetic basis to evolution and thus integrated genetics with evolution.

With the publication of Dobzhansky's book, the modern synthetic theory was born in 1937 as a generally accepted way of approaching the problem of evolution, although Huxley[8] used the term 'modern synthetic theory' for the first time in 1942. Dobzhansky is considered as the architect of synthetic theory of evolution. Ernst Mayr, G. G. Simpson and G. L. Stebbins have also contributed in the development of the concept of the modern synthetic theory of evolution. This theory was developed around the original concept of natural selection proposed by Darwin. However, it incorporates much which is post-Darwinian. It is called synthetic theory because it combines many factors in one hypothesis which brings about evolutionary changes. During the past many years, researches in the field of evolutionary biology have shown that elemental forces of evolution operate not upon individual genes or individuals, but that these forces act upon a group of individuals called population which consists of pooled genes of all individuals of a Mendelian population constituting a gene pool. Natural selection is the driving force of evolution which acts upon this gene pool. Thus population forms the stage for evolution on which evolutionary forces operate and during this process, the individual genes may be eliminated or reproduced and certain genotypic combinations may be favoured over others in the population. Thus evolution is any change in the genetic composition of a population. How the gene pool is modified and the allele frequencies change in the Mendelian population was an interesting question before the geneticists after the rediscovery of Mendel's laws in 1900. The question was: if in a Mendelian population with closed gene pool, there are two alleles of an autosomal locus (A and a) and their frequencies are p and q, what will happen to p and q in succeeding generations? This problem was considered by a few scientists, but no definite solution was given. The fundamental discovery about the nature of the gene pool and gene frequency was made in 1908 by G. H. Hardy, a mathematician from England and

W. Weinberg, a physician from Germany. They suggested a law, i.e. Hardy–Weinberg law or binomial square law or rule which states that under certain conditions, gene and genotypic frequencies will remain constant from generation to generation with genotypic frequency being determined by gene frequency. This law is used to determine the frequencies of each allele of a pair or of a series as well as the frequencies of genotypes (homozygotes and heterozygotes) in a Mendelian population. When the frequencies of genes and genotypes remain constant, the population is said to be in genetic equilibrium or Hardy–Weinberg equilibrium. Thus, Hardy–Weinberg equilibrium is a conservative force and does not allow evolution to occur. When this equilibrium is modified, evolution occurs. The factors or forces which modify this equilibrium are considered as important evolutionary forces. Modern synthetic theory is based on these elemental forces of evolution such as mutation, recombination, natural selection, random genetic drift, migration and hybridization. Genetic variability generated by mutation and recombination provides raw materials on which selection, drift and migration operate to bring about changes in population, and evolution continues.

Isolating mechanisms

This term 'isolating mechanisms' was coined for the first time by Dobzhansky[7] in 1937 and elaborated in detail in his book. The significance of isolation was recognized even during the time of Lamarck and Darwin. In 1868, Wagner proposed the theory of isolation to explain the mechanism of evolution. It has been mentioned that without isolation evolution is not possible. Isolating mechanisms include all those factors which alone or in combination prevent gene flow by preventing interbreeding between different Mendelian populations. Different types of isolating mechanisms have been described and discussed with suitable examples[7,9–14]. Dobzhansky[7] classified isolating mechanisms into different types. He classified them basically into two types: geographical or spatial isolation, and reproductive isolation. Geographical or spatial isolation operates between allopatric species/populations (populations inhabiting different geographical areas). Mating is prevented because males and females cannot cross the geographical barrier. When the species are allopatric in distribution, it is not necessary that they will show reproductive isolation. If in the course of time, they have not developed any kind of reproductive isolation, removal of the ecological barrier may lead to merger of two separate gene pools and the differences which they have acquired may be removed. Reproductive isolation operates between sympatric populations/species (inhabiting the same geographical region) which remain isolated by genetically conditioned barriers to gene exchange. Dobzhansky[7,15] classified reproductive isolating mechanisms between sympatric species into eight different types while mentioning suitable examples and also showing how different types may work in combination to prevent gene flow between populations: ecological isolation, seasonal or temporal isolation, sexual (behavioural or ethological) isolation, mechanical isolation, gametic isolation, hybrid inviability, hybrid sterility and hybrid breakdown. He discussed different kinds of reproductive isolating mechanisms providing suitable examples from different animal species. Dobzhansky gave much emphasis to *Drosophila* and a large number of examples are described in fruit fly in which two types: sexual isolation and hybrid sterility are discussed in detail[7,9,11,16,17]. He discussed hybrid sterility having genetic basis between *D. pseudoobscura* and *D. persimilis*, two closely related and sibling species[7,15,18]. Both the types of reproductive isolating mechanisms: sexual isolation and hybrid sterility have been extensively studied in different species of *Drosophila* and extensive data have been published showing evolutionary significance[11,17]. The pattern and degree of sexual isolation among different species of *Drosophila* have often been used to elucidate their phylogenetic relationship and even to predict the direction of evolution[12,19–22]. The phenomenon of hybrid sterility is also important from the evolutionary point of view and has been studied in detail in different species of *Drosophila*[17]. It becomes important in the area of speciation genetics because the genes responsible for hybrid sterility are called the speciation genes[17]. Thus the phenomenon of isolating mechanisms originally suggested by Dobzhansky[7] in 1937 is of much importance in the field of evolutionary biology as far as mechanisms of speciation are concerned. Thus Dobzhansky's book is important from both points of view: integrating genetics and evolution, and providing the basis for the modern synthetic theory of evolution which is the most widely accepted theory in which natural selection is the important guiding force of evolution, although it combines other factors like mutation, genetic drift, etc. which are post-Darwinian. Thus, Dobzhansky's contributions are important in the area of evolutionary biology for both aspects: providing genetic basis of evolution and in the development of modern synthetic theory of evolution. He rightly remarked 'Nothing in biology makes sense except in the light of evolution'[23]. This statement is really important because Darwin has already proposed that all the organic beings which have ever lived on this planet have descended from pre-existing ones. From this it follows that every characteristic of every species is an outcome of evolutionary history – character behaviour, DNA, feathers, physiology, biochemistry, nutritional requirements, eggs, sperm, reproduction, embryology, etc. The evolutionary perspective touches upon every subject in biology, from molecular biology to ecology and genetics. Thus evolution is the unifying theory of biology, confirming Dobzhansky's statement mentioned above.

Conclusion

It has been mentioned that evolution is the corner stone of biology. It touches every field of biology. The idea of evolution is not of recent origin. Even in Greek writings (600 BC), its essence was found but everything was vague and unacceptable. Naturalists and philosophers also believed that it is special creation by God which is unchangeable. For many centuries nothing was added. In this context the suggestion of Aristotle is important that living organisms are arranged in an order of increasing complexity like a ladder of life. As far as modern biology is concerned, it was Lamarck (1809) who could give the clear understanding of evolution that living organisms existing on earth are the result of evolutionary change. Although his theory of 'Inheritance of acquired characters or theory of use and disuse' to explain the mechanism of evolution was not acceptable and severely criticized. So the world had to wait for fifty years for a very important theory of evolution which was proposed by Darwin and discussed in his book *On the Origin of Species by Means of Natural Selection*. It was acceptable by a large number of biologists of that time. However, it has certain demerits and the important one is his lack of knowledge of genetics. He could not explain how variations arise and play a role in evolution. Now, we know that those variations which have genetic basis and are inheritable play a role in evolution. Dobzhansky[7] who published his book *Genetics and the Origin of Species* in 1937 provided the genetic basis of evolution discussing various topics in his book such as mutations in populations, Hardy–Weinberg equilibrium, balanced polymorphism, role of selection, genetic basis of hybrid sterility, isolating mechanisms, genetic coadaptation, role of inversion polymorphism in laboratory and natural populations of *Drosophila* which clearly provided the genetic basis of evolution. Thus through his work and concepts of population genetics he integrated genetics with evolution demonstrating how natural selection operates on genetic variability by his studies in laboratory and natural populations of *Drosophila.* Although the term modern synthetic theory was used later by Huxley[8] in 1942, Dobzhansky is considered the main architect of modern synthetic theory. Further, it has also been suggested that the modern synthetic theory as a generally accepted way of solving the problems of evolution took birth in 1937 with the publication of the book of Dobzhansky[7]. Thus Dobzhansky integrated genetics and evolution which is evident from the titles of two very important books: *Origin of Species* (Darwin) and *Genetics and the Origin of Species* (Dobzhansky). It has been said that Dobzhansky is the 20th century Darwin[6].

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