The Roles of Environment in Evolution

By

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With 1 Figure

1. Introduction

Charles DARWIN and Alfred Russel WALLACE are independently credited for the discovery of the principle of natural selection. But Darwin, the "Newton of Biology", stole the laurels all the way through, by backing his ideas with a tremendous amount of data that "rendered evolution

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inescapable as a fact, comprehensible as a process, all embracing as a concept" (HUXLEY 1960). Nevertheless the concept of evolution has been modified and extended considerably since the days of Darwin and "Darwinism" has given rise to "neo-Darwinism" and finally to "post-neo-Darwinism" (SIMPSON 1953a: 58) which may more appropriately be designated as "biological or synthetic" theory of evolution (DOBZHANSKY 1960). GRANT 1963 has opined that since "the theory of natural selection held by evolutionists at the present time is different from the selection theory of Darwin's time" ...... "it would be rash to assume that evolutionary theory a century hence will not differ profoundly from our present day concepts".

According to the currently accepted concept of the theory of evolution, the essential elements are (1) Variability, (2) Genetic Drift and Natural Selection. The sources of variability include (a) mutation, (b) recombination and (c) gene flow. Except in the case of small populations where Genetic Drift or Sewall Wright effect is operative, the selective role of environment is accepted as the major factor in evolution. Though there has been considerable change of emphasis, from rather more severe aspect, emphasized by DARWIN in terms of "struggle for existence" to a range of selection pressures, which may vary from slight rather imperceptible change to the most severe action finally resulting in the death and disappearance of some of the forms.

2. The roles of environment

It is generally accepted that the chief role of the environment is to act as sieve, favouring suitable genetic combinations and rejecting the less suitable ones. In view of these roles of the environment, which are actually two aspects of the same process, WADDINGTON 1957 alludes it to dual effect of environmental pressure and has also emphasized the fact that it is not the environment alone that plays the role of selection, the individuals particularly animals, also have a choice to select their environment. In the case of non-motile plants, which have to depend upon extrinsic agencies for their dispersal (through seeds etc.), the concept of the choice of the environment by the individual cannot be applied in the same sense. Further it is also established that the environmental natural selection not only results in the elimination of certain combinations, but the environment also induces certain adaptive changes (physiologic or morphologic) to enable the individual to survive in a particular type of set up. Presently, it seems that enough data has accumulated to make it possible to attribute yet another role to environment i. e. its role in the production of variability by affecting the mutational frequencies or by acting on various components of recombination system and gene flow.

3. Mutation

It is generally accepted that the basic source of variability, that is so essential for evolution, is mutation. Mutation can be considered at three different levels (1) gene (2) chromosome (3) chromosome set or genome.

3.1. Mutagenic agents

Under normal conditions genes mutate at a certain frequency, which is known as the spontaneous mutation rate. The mutation rate is generally increased when the organism is exposed to x-rays, ultraviolet light, mustard gas and some ionizing radiations (GRANT 1963). Treatment with certain chemicals, fertilization with "stale" pollen, mutilation, and the use of long dormant seeds, also increases the mutation rate (TURRILL 1940). NICHOLAS 1941 and D'AMATO 1963 have also shown that decrease in germinability with increasing age of seeds is accompanied by progressive increase in chromosome abberations and mutation frequency. Heat definitely increases mutation rate; some types of mutations increase towards extreme low temperatures also (SRB & OWEN 1952). STEFFENSON 1953, 1955 has shown that in *Tradescantia*, spontaneous breakages increase when medium is deficient in Calcium and Magnesium. Translocation in flowering plants can be produced by means of puterscin, a product of natural decay from oil seeds. ABRAHAM 1965 has shown that decaying organic substances, like compost, cow dung and oil cakes can cause chromosomal and genic changes. Similar changes are also induced by substances like ammonium sulphate, ammonium nitrate, ammonium phosphate and potassium chloride. It is extremely significant that these substances are normally used in agricultural practices and are components of the natural environment.

3.2. Genotypic control of mutation

Mutations may be gene controlled (BEADLE 1922, IVES 1950, McCLINTOCK 1950, 1953). "The genotypic control of mutability would account for some of the characteristic differences that have been found in the spontaneous mutation rates of some of the organisms" (GRANT 1963). McCLINTOCK 1956 demonstrated the presence of mutation and gene action controlling elements, situated on the chromosome in maize and suggested that "controlling elements are normal components of chromosome complement and that they are responsible for controlling, differentially, the time and type of activity of individual genes".

It has been argued that the higher organisms do not normally encounter mustard gas and other mutagenic chemicals in their natural external environment, and the radiation to which they are exposed naturally, is not enough to explain the frequency of mutation. GRANT 1963 has suggested that these organisms "do perhaps come in contact with chemical mutagens of their own making in the internal milieu of the cell".

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Biochemically "a gene corresponds to a number of nucleotide pairs" (FREESE 1959). Change in one nucleotide pair is enough to cause gene mutation. Mutation has also been defined as chance imperfection in gene duplication (GRANT 1963). According to DOBZHANSKY, SPASSKY & SPASSKY 1952, it is difficult to understand why two closely related species, *Drosophila willistoni* and *D. prosaltans* should exhibit very different mutation rates under similar environmental conditions, if the mutability of a species is the sum total of the chance imperfections in gene replication. This difference in the mutation rate of two species of *Drosophila* can however be explained on the alternative view that mutation rate is genotypically controlled and that this has been adjusted by natural selection in each species according its particular circumstances. Thus an alternate hypothesis is available, according to which mutation rates are due partly to selection rather than solely to chance (GRANT 1963). Further, it can be argued that no evolution could take place without the available variation and that most types of variations, basically depend upon mutations. If it is true that mutations are merely chance imperfections in gene duplication, it leads us to believe that the production of variation is fundamentally based on imperfections or mistakes in replication. Thus an important pillar of the foundation of the grand edifice of the theory of evolution seems to be dependant upon imperfections or mistakes in a particular life process. In view of the universality and the importance of the process of evolution in the progressive development of the organic world, could there be any more ironic situation!

3.3. Environment and mutation

From the evidence available, one could generalize that like all other character expressions, all mutations take place as a result of the interaction between the genotypic composition of the individual and the environment. One should also admit that the distangling of these two variables is an impossibility because one cannot study the effect of one in the total absence of the other. Therefore it is not justifid to generalize that spontaneous mutations are gene controlled and induced mutations are not. To be more precise, it is desirable to express even the spontaneous mutations in terms of the environmental background concerned.

Further it seems that some factors which form an integral part of the normal environment contribute to the production of mutation as a normal routine. Factors like temperature and substances that normally contribute to the nutritional requirements of the plant (STEFFENSON 1953, 1955; ABRAHAM 1965). Though this cannot be said for all the other environmental factors at the moment, is it due to lack of information in this respect because enough attention has not been paid to this problem ?

It is also interesting to note that the use of mutilated or long dormant

seeds results in the increased mutation rate. This seems to be of tremendous evolutionary significance. Because, in nature, if a seed is not able to germinate in a proper environmental complex, it obviously, is an indication of the fact that the environment concerned is not suitable for seed germination and even if the seed is able to germinate, it may not be able to survive under such conditions. Under these circumstances, the surviving potential will increase many folds, if the organism concerned could modify itself. Hence the importance of increased rate of mutation under these conditions. In this connection it may be pertinent to repeat the remark of TURRILL 1940 that "mutations" are of all "sizes" and owe their origin to one or other of a variety of "causes", some of which are "constituents of the ever varying natural environment, suggests strongly, to an experimental taxonomist who is not biased by acceptance of the views of any extreme school of evolutionists or phylogenists . . .".

3.4. Directed mutations

Though WADDINGTON 1957 suggested "that it may be unsafe to consider that the occurrence of directed mutation related to environment can be ruled out of court a priori", presently people do not believe in the occurrence of directed mutations. The work on microorganisms has increased our understanding of some of the aspects of this phenomenon considerably. It is possible to develop resistant strains in any type of bacteria provided the number of individuals exposed to the bacteriophage to which they are susceptible, is large enough to make it possible for the resistant type of mutation to arise, and provided such a mutation can possibly take place in the organism concerned (DOBZHANSKY 1960). The work of LURIA & DELBRUCK 1943, DEMEREC & FANO 1945 and LURIA 1946 and others on the colon bacteria, *Escherichia coli* may be referred in this connection.

It seems necessary to discuss further, the desirability or otherwise, of directed mutations in the organic world. Firstly, it is quite obvious that, in response to a particular environment if the production of only those mutations which are likely to be selected, was the rule, it will lead to more and more specialization which will result in the elimination of many genes in due course of time, in direct response to natural selection. It is an established fact that overspecialization, though useful for a particular environmental set up, imposes many restrictions on the organism and may ultimately result in its undoing, in the face of unfavourable circumstances. Secondly the inter-relationships that exist between the environmental complexes in nature, are extremely complicated and should never be presented as linear variations in any one factor. For instance the increase or decrease in temperature for a certain period will also result in the movement of air, the difference in humidity, change in relative atmospheric pressure, change in soil temperature, change in the rate of evaporation of water

from the soil and thus change in the concentration of soil nutrients; change in the microflora frequency present round the organism etc. Thus it is obvious that environmental stresses are never simple. These stresses are also subject to constant change, so much so that the change which is required in response to the environment at a particular time may loose its importance by the time the organism is able to precipitate it, because there is always a lag period between the cause and the production of the so called effective mutation. For instance Newcombe 1956 has demonstrated that in *Streptomyces* ultra violet induced mutations are not completed until after some considerable delay. The mechanisms operative in higher organisms is expected to be more complicated and time consuming. Therefore it seems logical to conclude that simple directional mutations will not be able to meet the requirements of the dynamic, ever changing environmental complex. The only possible mechanism that could take care of the dynamic situation is the production of plentiful multidirectional mutations. The only draw back in this system is the waste of large number of individuals which are not selected for. But this is a compromise that seems inevitable.

4. Environment and the recombination system

It has been pointed out by Darlington 1939, Mather 1943 and Grant 1958 that the genetic system is also subject to natural selection and adaptation. This is substantiated by the presence of diverse types of recombination systems in nature. Each type seems to be most suited to the conditions of the organism possessing it. Further, phylogenetically unrelated organisms are known to possess similar genetic systems. This is most satisfactorily explained by assuming that the common characteristics have evolved under control of common selective factors. Therefore it is reasonably probable that different types of genetic systems have evolved as products of environmental selection (Grant 1958).

Grant 1958, while reviewing the factors which regulate recombination in plants, has listed nine factors under three main headings. Almost all these factors are affected by the environment, but some of the factors like "frequency of crossing over", "sterility barriers", "breeding system" etc. are such which seem to have more direct role in the regulation of variability. It is very well known that crosses between compatible gametes that are not conducted under suitable environmental conditions are not successful. Should this be looked upon as a natural check to avoid unnecessary wastage in the face of adverse environmental conditions? It is also known that 17° C rise above normal for 48 hours in *Allium cepa* resulted in drastic reduction in chiasma frequency, failure of normal segregation, lagging chromosomes, micronuclei, bridges and failure of synapsis (Alam 1966). Similarly the effect of low temperature (0° C) on meiotic chromo-

somes in *Trillium kamtschaticum* resulted in increased interstitial chiasma frequency at metaphase I and bridges were formed due to chiasma breakage (LIU & MATSUURA 1967).

5. Gene flow

Gene flow is one of the mechanisms by which a population can acquire additional variations. Gene flow obviously depends upon the dispersal potential of the individuals or the gametes. The capacity of motile individuals to select their environment (WADDINGTON 1957) may also result in gene flow. Gene flow, particularly that aspect which is concerned with the migration of individuals, is the result of the adjustment between the available environmental complexes and the migratory potential of the individuals. Here the equilibrium is reached not only because of the environmental selective action on the available variability, but because of the interaction of the factors referred above. The selection of habitats by motile individuals is not only inferred, it has been experimentally demonstrated by WADDINGTON, WOOLF & PERRY 1954, using *Drosophila melanogaster*. They devised an apparatus, consisting of a central compartment connected by tunnels with 8 peripheral chambers. Each of these chambers had different environmental conditions. Known number of normal and mutant flies were introduced into the central compartment at the beginning of the test and left to themselves for 5—6 hours. After this time numerical distribution of flies in different chambers was recorded to prove that different genotypes had different environmental preferences.

The role of environmental conditions (like wind velocity etc.) which can affect the dispersal potential of animophilous pollen grains and seeds also plays an important role in facilitating gene flow. It may be pointed that mere presence of an individual, propagule or gamete in a new environment does not constitute effective gene flow unless the new genetic material is incorporated in the gene pool of the population. For instance, it is known that the long distance transport of pollen by wind in *Pinus* and *Tilia* is without genetical effect because the period of receptivity of the pollen is limited and does not always coincide at the two places (WETTSTEIN & ONNO 1948).

6. Inheritance of acquired characters

The theory of the inheritance of acquired characters as held by LAMARCK, DARWIN and other traditional authors postulated that environmental influences affecting the body parts were supposed to be transmitted to future generations (GRANT 1963).

There is evidence that hereditary diseases are both acquired and inherited. Mutations acquired during the life time of an individual will be passed on to its progeny if they occur in the gamete producing cells (GRANT 1963). It has been demonstrated in the case of *Euglena mesnili* that in some lines of individuals which were constantly grown in dark,

the chloroplasts were lost completely. The chloroplasts did not reappear even when the organism was subsequently exposed to light, as in the case of *E. gracilis* (Lwoff 1950; Haldane 1954). In *Euglena mesnili* an externally directed hereditary alteration is possible because the phenotype coincides with the genotype in this case (Grant 1963). The cases of hereditary transformations and transductions are known in bacteria. In both these cases the heritable properties of the particular strain are changed (Avery, Macleod & McCarty 1944; Dean 1958; Zinder 1958). The processes of transformation and transduction in bacteria have no known counterparts in higher organisms except the hereditary disease organisms which introduce foreign genetic material into the body of the host with results that are perpetuated in the progeny (Grant 1963).

In the case of higher multicellular plants, it is hypothetically possible to visualize that environmental stimuli may influence the reproductive as well as somatic cells situated on the shoots in such a way that the responses are transmitted, though as yet this has not been demonstrated (Crosby 1956). Crosby 1956 has postulated the role of cytoplasmic genes in this connection, though the process is not properly understood (Michaelis 1954).

Inspite of the cases cited above, the theory of inheritance of acquired characters is, by and large, invalidated by both the embryological and genetic evidence (Grant 1963). This does not mean that the acquired characters do not play any role in evolution. For, it is well established that selection acts on the phenotype and acquired characters are directly concerned with the modification of the phenotype.

Furthermore, though the acquired character may not be transmitted genetically, nevertheless there is strong probability of the inheritance of the potentiality of acquiring similar characters under similar environmental stress, from parents which are endowed with the potentiality of acquiring certain adaptive characters under certain environmental conditions. The evolutionary significance of this potentiality will be discussed further with reference to "the Baldwin Effect" and the ideas of Waddington 1957, 1960 that have been advanced in this connection.

7. The Selection Pressure and Adaptive mechanisms

It is not necessary to emphasize the role of selection pressure in terms of "struggle for existence" and "survival of the fittest", as done by Darwin. It is possible to visualize various types of adaptive mechanisms and their probable correlation with the intensity of selection pressure. Such a classification of the selection pressures is purely arbitrary and the various recognized groups merge into each other. Similarly a transition may be observed between various types of adaptive mechanisms operative under various selection pressures.

7.1. Physiological homeostasis

The populations may remain constant phenotypically, but react physiologically in order to come to an equilibrium with the environment. This property of organic stability under variable environmental conditions is known as physiological homeostasis (GRANT 1963). Examples may be given of the human body which reacts to cold by shivering and to heat by sweating. In the case of plants the fluctuations in the rate of transpiration under various conditions of wind velocity or various gradients of temperature, may be referred in this connection. Irrespective of the intensity of selection pressure, the first stage of adaptive mechanism is invariably the physiological homeostasis. Physiological homeostasis may be enough to take care of low environmental selection pressure, however, in the cases of more severe selection pressures, in addition to physiological homeostasis other types of adaptations may be called for. The pattern of adaptive mechanisms in such cases is different in the case of motile and non-motile individuals and also in the case of animals and plants in view of their different growth patterns. These adaptive mechanisms have been discussed under the following headings:

7.2. Selection of habitats

The motile organisms are capable of discarding the unsuitable environment and migrate to more suitable places. The migratory potential of the individuals and the availability of suitable habitats are important in this connection. Some aspects of this problem have already been discussed under gene flow.

7.3. Environmentally induced phenotypic modifications

Before discussing the evolutionary significance of this phenomenon, it seems desirable to discuss some generalized differences between plants and animals. In the case of animals the morphological pattern of various organs is decided at the time of the development of the zygote into the individual. The individual is capable of growing further for a certain time. During this period, the organs grow in size, without affecting the overall morphology of various organs. Each main organ of the body is formed once during the life time of the individual (barring the cases of regeneration of organs observed in certain groups like *Crustacea* etc.).

In the case of plants, in most of the groups the individual is capable of almost unlimited growth throughout its life. The leaves which are the centres of most of the vital activities, are replaced continuously. The younger leaves and branches formed under different environmental conditions, are capable of exhibiting appropriate phenotypic modifications, in response to respective environmental stresses. Thus the potentiality

of phenotypic modifications in the case of plants is far more than in the case of animals.

The effects of environmental influence on the phenotypic expression of the plants have long been investigated but it is to the credit of pioneer genecologist TURESSON to have given these studies direction and meaning. Since the outstanding publications of TURESSON 1922a, 1922b, 1923, 1925, 1930 workers like GREGOR 1931, 1939, 1944, CLAUSEN, KECK & HIESEY 1940, 1945, 1948, CLAUSEN & HIESEY 1958, SINSKAYA 1942, 1958, 1961, 1963 and others have contributed tremendously to this problem. The phenotypic changes, which are being discussed here have been referred to as ecophene (TURESSON 1922b) or ecad (CLEMENTS 1908). The importance of the environmentally induced phenotypic changes is obvious, because, in addition to physiological homeostasis, by virtue of presence of this quality the plant is able to adjust and survive under unfavourable circumstances. Generally speaking, there seems to be an inverse correlation between the motility of the individual and the production of environmentally induced phenotypic modifications. It seems that the absence of environmentally induced phenotypic plasticity is evenly balanced in the case of animals by their ability to migrate to a more suitable habitat.

7.4. Genotypically induced phenotypic modifications

There is overwhelming evidence, particularly from the plant world, which indicates that if the environmental stress, responsible for the production of a particular phenotypic modification, persists for some time, there is a likelyhood that the said modification may become genetically fixed. Such genetically fixed modifications are generally designated as ecotypes. Workers have also come across mixed populations of ecophenes and ecotypes as in the case of *Succisa pratensis* (TURESSON 1922b) or *Senecio lautus* (ALI 1964) etc. Such intermediate cases indicate that the transition from environmentally induced to genetically fixed modifications, is gradual. The environmentally induced modifications continue to buffer the selective pressure, till similar adaptations, are finally genetically fixed.

In the case of animals, as the developmental pattern of the individual is fixed during the development of the zygote, the environmentally induced phenotypic changes can only be investigated in terms of the stimuli received at this stage. WADDINGTON 1956, 1957, 1960 has demonstrated that the exposition of pupae of *Drosophila melanogaster* to high temperature, resulted in the adult flies with wings lacking a posterior cross vein and the treatment of eggs with ether produced some "bithorax" individuals. Genetic mutants having these features are also known in nature.

The treatment of eggs with ether in each generation resulted in the production of some bithorax individuals. Some of these bithorax individuals were selected as the parents of the next generation. The eggs were again

treated with ether, which resulted in the production of some bithorax individuals. This process of treatment and selection was continued for 29 generations.

In a separate parallel experiment the normal phenotypes were subjected to the same treatment for the same number of generations.

In each generation of both selection lines some eggs were allowed to develop without ether treatment. In the bithorax line in the eighth generation one fly from an untreated egg showed slight tendency of bithorax condition. In the ninth generation 10 bithorax flies appeared and in the 29th generation several such individuals arose from untreated eggs. The fact that this character is genetically controlled in these individuals was confirmed by progeny tests. In some of these, specially the mutants obtained in 29th generation, the bithorax phenotype was determined by a major allele and modifier genes (WADDINGTON 1956).

Similar experiments conducted for the crossveinless condition, demonstrated that this character is genetically fixed in some of the individuals after selection for 24 generations. Here also the heritable condition of crossveinlessness appears to be determined by a major gene and modifiers.

STERN 1958, 1959 has advanced the explanation which postulates the presence of certain genetic factors which remain unexpressed in the original environment, but come to expression in the modified environments. This results in the production of bithorax condition or the modified wing. In the new environments where the genetic factors were being expressed, the selection could alter their frequencies. The selection of such genes which had strong modified phenotypic expression in an abnormal environment had the collateral effect of building up genotypes which produced the mutant phenotypes also in the normal environment. BATEMAN 1956, 1959 independently advanced similar explanation and suggested that types of genetic factors being favoured with selection may be penetrance modifiers, which exhibit incomplete penetrance at the beginning, but bring about more complete penetrance later on. GRANT 1963 has elaborated the idea of penetrance or expressivity modifiers further and has pointed out that "the potentialities of phenotypic expression which can be created inadvertently by selection in one environment, may sometimes have important consequences in evolution, as where a population becomes prepared or 'preadapted' in an ancestral environment for entering a new environment".

In connection with the discussion of the genetic fixation of acquired characters reference may be made to the Baldwin Effect or the theory of organic selection (SIMPSON 1953b). According to the Baldwin Effect the organisms have the potentiality of producing non-hereditary adaptations in response to the new environment. Genetic factors producing similar traits occur in population and these factors increase in frequency under

natural selection. WADDINGTON 1957 has pointed out that the flaw in this hypothesis lies in the absence of any connection in the production of adaptive characters in response to an environment and the production of mutation having similar effect, even in the absence of the environment concerned. The explanation advanced by WADDINGTON 1953, 1956, 1957, 1960 takes into account the lowering of threshold, as a result of the production of environmentally induced modification, thus "requiring only a small gene mutation or, eventually a single specifiable mutation" to bring about genetic fixation of the same trait. Nevertheless according to GRANT 1963 it does call for the production of mutations that are oriented with respect to adaptive requirements of the organisms (GRANT 1963). However, it is known that environmental conditions do affect mutation rates. Unfavourable environmental conditions, where the organisms are able to survive by producing some phenotypic adaptations, are likely to alter the mutation rates considerably, so that the individual may have a better chance of selecting the desirable mutants. In case where the potentiality of producing a particular adaptive trait under certain environmental stress already exists, it not only facilitates the survival of the individual in an unfavourable environment long enough to give it a chance to select the suitable mutants, but it also makes it possible for the organism to be continuously exposed to the unfavourable environment which is likely to result in changed frequencies of different types of mutations. Thus we do find connection between the potentiality of an organism to exist by virtue of producing adaptive characters in a new environment and the role of this potentiality in being instrumental in increasing the mutations. The advantage of not having only directed mutations has already been discussed earlier, where it has been shown that the production of only directed mutations is not in the wider interest of the organisms in view of the dynamic situation with which it has to cope with from time to time.

In a case where a particular adaptive trait can be produced as a result of the environmental stress, the only change that is required is the shift to a situation where the same character could be produced even in the absence of the stress concerned. The mutation required for this purpose is expected to be a minor one, as stated by WADDINGTON 1960. The probability of the production of this type of mutation in such a system is not expected to be low.

It seems that all cases where synthesis of ecotypes exhibiting adaptive environmental traits, has taken place, are synonymous with the genetic assimilation of acquired characters. In view of the wide spread nature of this phenomenon in the organic world, more than one genetic mechanisms are likely to be playing their role. Hence there is room for the suggestions

of STERN 1958, 1959, BATEMAN 1956, 1959 as well as for the Baldwin Effect or Baldwin — Lloyd Morgan hypothesis, in order to explain such phenomena.

8. The Evolutionary System

While presenting "the logical structure of the evolutionary system", WADDINGTON 1960 has discussed the role of the epigenetic system. WADDINGTON 1960: 400 has defined "the epigenetic system" as "the sequence of causal processes which bring about the development of the fertilized zygote into the adult capable of reproduction". This definition of the epigenetic system is adequate enough for most of the animals because here the developmental pattern is decided during the development of the zygote into an adult. But as this concept is applicable in the case of plants as well, where the growth pattern is not fixed during the development of the zygote into an adult, it is desirable to broaden the scope of "the epigenetic system", which may be defined in such a way as to include all "the developmental potentialities of the genotype". WADDINGTON 1960: 393 uses the phrase enclosed in inverted commas in connection with the definition of the epigenetic landscape. Thus 'the epigenetic system' is concerned with the sequence of causal processes which deal with the developmental regulation of the organism'.

According to WADDINGTON 1960, at least four major subsystems are involved in the evolutionary system. These subsystems are (1) the genetic system, (2) the natural selection, (3) the exploitive system and (4) the epigenetic system. The genetic system and the natural selection have already been discussed earlier. The exploitive system comprises of the sets of processes by which animals choose and often modify one particular habitat out of the range of available environments. In the case of non-motile organisms the question of the selection of the habitat does not arise, but the modificatory influence of the organisms on the total environmental complex can hardly be over emphasized (BATES 1960). As the environment that comes under focuss in connection with the exploitive system, is the same which plays the role of natural selection, it seems logical to recognize "the environmental system", with two components (1) the exploitive component and (2) the natural selective component. The role of the environmental system seems to be all embracing. The environmental system may (1) act on the genetic system, either by way of affecting the mutational frequencies or affecting various components of the recombination system. This may result in the alteration of the existing pattern of variation, and/or (2) it may act as selective force and thus be responsible for (a) the physiological homeostatic adjustments of the organism and/or (b) the production of adaptive (or retention of apparently non-adaptive if the character concerned is strongly canalized) morphological features. This aspect is con-

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cerned with the reaction of both the components of the environment on the epigenetic system. Thus we find that the environment not only acts as selective force and modifies the phenotypic frequencies (and thus indirectly the genic frequencies), it is also partly responsible for the production of various types of variations, which are subsequently subjected to its own selection pressure. The individuals that may be modified and selected, in their turn affect the exploitive component of the environment thus bringing about a change in the selective force. These ideas are diagrammatically presented in Fig. 1.
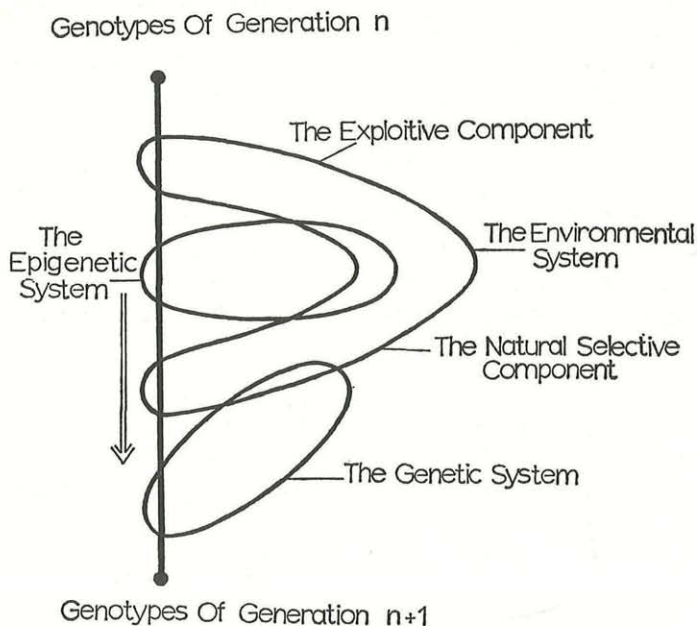

Fig. 1. The logical structure of the evolutionary system. Changes in gene frequency between successive generations involve the interaction of three systems.

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10. Summary

The multidirectional roles of environment in evolution are discussed. It is shown that the environment not only performs the role of natural

selection but it is directly concerned with the production of variability by affecting mutation and recombination. The disadvantages of unidirectional mutations are discussed. A generalized correlation between the power of motility and plasticity of the individual is indicated. Data from the botanical and zoological worlds dealing with the genetic fixation of acquired characters is equated and discussed. The structure of evolutionary system is also elaborated.

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