POLYPHENISM–GENETIC OR EPIGENETIC?

K. K. VERMA

M.P. Govt. Colleges, HIG 1/327, Housing Board Colony, Borsi, Durg   491 001, India
E-mail : kkverma.sheel@gmail.com

INTRODUCTION

In the post-Darwinian period genes have been considered as of prime importance in the development of the phenotype. But now again the role of genes along side that of the environment is being discussed, and some authors have even turned to Lamarckism. But one desirable aspect of this change, as pointed out by West-Eberhard (2006), is that the current discussion in this area has helped identifying "an important shortcoming of mainstream evolutionary thought, namely neglect of environmentally induced variation, and its importance for evolution by natural selection ...."

In the present context by 'genetic' is meant accountable by the Synthetic Theory of Evolution, which attributes all phenomena of inheritance and evolution to three factors, mutation, selection, and isolation. " 'Epigenetics' is the study of heritable changes in a gene expression and function that cannot be explained by changes in DNA sequence" (Bossdorf *et al.*, 2008).

" 'Phenotypic plasticity' refers to the ability of genetically identical organisms to alter their phenotype in response to an environmental change" (Anonymous, 2005) Some species exhibit more of phenotypic plasticity than others.

At present evidence in support of the genetic mechanism of phenotypic plasticity is dominant and overwhelming, and that supporting the epigenetic side is scanty. But significance of an open minded approach in this discussion cannot be over-emphasized.

GENETIC CONTROL OF PHENOTYPIC PLASTICITY

(i) Polyphenism in tobacco hornworm

A significant paper on a case of polyphenism is by Suzuki & Nijhout (2006). The larvae of the tobacco hornworm (*Manduca sexta*) are monophenic and green in colour. The larvae of a closely related species, the tomato hornworm (*Manduca quinquemaculata*) are polyphenic; they may be green, black and with intermediate body colours. The larvae of this species are black, if developed at 20° C, and green at 28° C.

Suzuki & Nijhout (*loc. cit.*) have concentrated on *Manduca sexta*, and have found that, if the larvae of this species are heat-shocked, i.e. by exposure to heat for 6 hours just before start of the moult between the 4th and the 5th instars, a range of body colours are produced, from black to the original green. As Verma (2007) has described, Suzuki and Nijhout performed the following experiment; " Among the larvae obtained in this manner (i.e. after the heat shock treatment), selection was done along two lines—a monophenic line by selecting black larvae in each generation to obtain the next generation, and a polyphenic line by selection of normal green larvae. In each generation nearly 3000 larvae were reared, and subjected to heat-shock. Of these, 60 larvae were then chosen, following the above mentioned body colour criteria, to get the next generation. A control line was also maintained; these were subjected to heat-shock in each generation, and the next generation was reared without any selection. The monophenic line lost its response to heat treatment after about the seventh generation, i.e. now heat treatment led to the production of only black larvae. In

the polyphenic line the body colour remained green even at 28° C. In the control line the body colour showed continuous variation between the black colour.... and the nearly complete green colour...." The observation in the control line suggests a polygenic control of development of body colour, and that the repeated heat treatment environment did not alter the polygenic response. Obviously the polyphenism in *M. sexta* is under genetic control.

(ii) Polyphenism in bruchids

Several workers have studied polyphenism in stored legume bruchids. In *Callosobruchus maculatus* F. and *C. analis* F. there are 'flightless' form (referred to as 'A' phase by Tiwary and Verma, 1989, a, b, and c) and George and Verma (1994, 1997, and 1999), and 'flight' phase (called 'B' phase by Tiwary and Verma, *loc. Cit.*, and as 'B' 'X' and 'Y' by George and Verma, *loc. cit.*). The 'B' individuals are highly melanic and are active flyers and 'A' are light coloured and less active. In between the two phases are a series of intermediate forms. Crowding or a high density population in a culture increases the proportion of melanic form (Tiwary and Verma, 1989c). That crowding has this effect has been observed also by Utida (1965). George and Verma (1999) reared *C. maculatus* in laboratory in medium density cultures, some at >40° C and high humidity (RH >90%), and some at 32+/- 2° C and RH 70 -75%. They noted a significant increase in the proportion of the melanic phase under conditions of high temperature and high humidity. It is believed that larval crowding in a legume store produces both a rise in temperature and in humidity.

Tiwary and Verma (1989c) did selection in high density cultures of *C. analis* for 10 generations, in 3 lines in favour of 'B' or highly melanic phase, and in 3 lines in favour of 'A' phase or lightly melanic phase. After the 10th generation in each line the bruchids were left to them-selves, i.e. without any further selection. In cultures, in which selection had been done for 'B' in the second post-selection generation all individuals were 'B' and in the cultures, in which selection had been in favour of 'A', out of 150 individuals, examined, all, except 2, were 'A'. Occurrence of intermediate forms between 'A' and 'B' in an unselected culture suggests a polygenic control in the phase development in the two bruchid species. Tiwary and Verma (1989d), from their experiments, have inferred that the significance of the 'B' phase of *C. analis* is that the individuals in this phase, being more active flyers, help in reaching new stores, when the original store has become too

crowded. Presumably on reaching a new store 'B' individuals breed and eventually produce a mixed phase population with 'A' dominating. This suggests that the effect of the environment in the original store is not inherited by the progeny in the new store. Obvious inference is that the control of polyphenism in bruchids is genetic.

(iii) Polyphenism in a pierid butterfly

Karisson (2008) has recorded in a pierid butterfly that "summer generation adults have a higher dispersal capacity measured as flight duration at five different temperatures" These summer adults have a larger thorax. About reproductive output, the summer females lay fewer eggs than spring females. Thus there is a trade-off between flight ability and fecundity. A similar trade-off has been noted in bruchids *Callosobruchus analis* (Tiwary and Verma, 1989a) and in *C. maculatus* (George and Verma, 1994). The 'flight' or 'B' phase females of the two bruchid species, though more active, have reduced ovaries and lower fecundity than 'A' or 'flightless' females.

Both in the stored legume bruchids and in the pierid butterfly there are shifts in the frequency of the phases with changes in the environmental conditions, because of cost of plasticity (Crispo, 2007). Such cases of polyphenism do not support the epigenetic concept.

(iv) Y-induced polyphenism

Lemos *et al.* (2008) have experimentally investigated the role of the Y chromosome induced polyphenism in *Drosophila melanogaster* flies. Thermal tolerance differs among different populations of the fly. Among *Drosophila* species "thermal heat sterility thresholds differ across species from 23° C in heat sensitive species upto 31° C in heat tolerant species" The thermal sterility in the fly results from disturbed spermatogenesis. For these experiments the authors have developed specially prepared strains of *D. melanogaster*, some with the Y chromospme from temperate climate (Ymass), and some with Y chromosome from tropical climate (Ycongo). (Ymass refers to the Y chromosome derived from flies collected in Msssachusetts, USA, and Ycongo to the Y chromosome derived from flies in Congo, Africa). In these strains the rest of the genotype or extra-Y genotype was homogenic. Flies of these strains were reared at 16° C and at 25° C. In either of the two strains some genes were up-regulated and some down-regulated at the two temperatures. "We (the authors) found that the Ycongo line showed about twice as many genes up-regulated at 16° C relative to Ymass, whereas the Ymass line showed about twice as many genes up-

regulated at 25° C relative to Ycongo...." From their studies the authors have concluded, "Our findings provide a mechanism for adaptive phenotypic variation associated with the Y chromosome"

(v) Chirality in snails

In most snail species individuals have dextral shells, and sinistrality of shells is rare. But the west Asian snail *Amphidromus* shows the two enantiomorphs in considerable proportions, the frequencies of the two varying in different populations, proportion of sinistral individuals reaching even 90% in some cases. Schilthuizen *et al.* (2007) have studied this snail, and have found the reasons for the high frequency of sinistrality. The reasons are: (1) Interchiral matings (i.e. matings between dextrals and sinistrals) occur in *Amphidromus*, whereas such matings are not known in other snails, and (2) Such interchiral matings result in greater fecundity, which means selective advantage for such matings. In this instance the shell dimorphism is obviously genetic.

(vi) Cavefishes

Borowski (2008) has experimentally studied the blind cavefish, *Astyanax mexicanus* in 29 different caves in north-eastern Mexico. This fish with normal vision occurs in surface waters too. From various experimental crosses the author has inferred that the loss of vision has been due to mutation at different loci in the cavefish populations in different caves. Twelve such loci have been identified (Niven, 2008). On crossing a surface fish and a cavefish, in the resulting F1 generation the fishes have been found to have smaller eye than in the surface fish, but fully visual. F1 hybrids, from a cross between a cavefish from the Tinaja cave and a fish from the Molino cave, have been found to have 39% vision. It has been estimated that the fishes reached the caves in mid-Pleistcene, i.e. about 1,000,000 years back.

Main inferences arrived at in Borowski's study :

(1) Loss of vision in the fish in the dark environment of the caves evolved independently in different cave populations through convergence,

(2) The loss of vision has been through mutation at multiple loci,

(3) It is likely that the reduction of eyes has been through genetic drift in the absence of selection pressure to maintain eye function.

Though Lamarckists, like R. Jeannel, have often cited the example of blind cavefishes in support of their notion, in the study of the Mexican cavefishes by Borowski (*loc. cit.*) there is little to support either Lamarckism or epigenetics.

(vii) *Heliconius*, a markedly plastic butterfly

Butterflies of the Neotropical genus *Heliconius* present a remarkable example of phenotypic plasticity (Kronfrost and Gilbert, 2007). They present "hundreds of distinct mimetic wing patterns at both population and species level" *Heliconius erato* and *H. melpomene* are an instance of a pair of mimetic species with nearly identical wing pattern, and sympatric in distribution. How has this sympatric diversity evolved? To explain this the authors have hypothesized that *Heliconius* species have subpopulations within the range of a population. Within a subpopulation genetic diversity arises followed by the Sewall-Wright effect or local genetic drift. As a result of the drift certain mutant genes start increasing in frequency. When in frequency they reach a threshold value and are of defensive significance, they get "protected" by which the authors seem to mean through natural selection.

The 'subpopulation' part of the hypothesis has been confirmed by Kronfrost *et al.* (*loc. cit.*) by taking to mark-recapture method. They have inferred that the butterfly shows a small home range behaviour; hence isolated subpopulations.

To confirm the 'genetic drift' part of the hypothesis Kronfrost *et al.* have done DNA analysis. From such studies they have inferred "local genetic drift over very limited spatial scales" Thus ployphenism in *Heliconius* butterflies is essentially a genetic phenomenon.

(viii) A case of *Chrysochus* leaf beetles

Dahlhoff and Rank (2007) have studied a case of physiological polyphenism in the mountainous leaf beetle *Chrysochus aeneicollis* in three different areas in Sierra Nevada, California. The three areas have named as BC, BPC, and RC. RC is at the highest elevation and BPC at the lowest, while BC is at a middle elevation. Mean summer temperature is lowest at RC, and highest at BPC. The authors, in their study, have concentrated on the enzyme locus phosphoglucose isomerase (PGI). This enzyme is involved in temperature tolerance. Two alleles of the enzyme locus have been identified, PGI-1 and PGI-4. In the beetles in the area RC PGI-1 dominates, and PGI-4 is only small in proportion. In BC PGI-1 is more, but PGI-4 is more in frequency than in RC. In BPC PGI-4 dominates. The authors have studied the frequency of PGI alleles in 1988 and in 1996. They have found that "During that time the frequency of PGI-1 increased by 11% in BC, while PGI-4 decreased. These directional shifts did not occur at other polymorphic

enzyme loci, suggesting that changes at PGI resulted from natural selection favoring PGI-1 allele" Role of genetic mechanism in this case pf physiological polyphenism is obvious.

(ix) Gorilla polyphenism

Anthony *et al.* (2007) have studied mtDNA variation among different gorilla populations, and have found that the results support the view that the genetic variability among the populations has resulted from their distribution among the patches, formed by the Pleistocene fragmentation of the forest, providing refugia to forest dwelling species, and from river barriers. They point out, "Admixture is also evident along the borders between refugial populations" Morphological and behavioural polyphenism among gorilla populations in such border areas is obviously genetic in origin.

(x) Polyphenic yeast

It has been known for quite sometime that some strains of yeast are phenotypically more plastic with environmental changes than others. Some 6000 genes in yeast have been studied as to their response to variety of stressful environments. It has been found that that genes vary enormously in their response to varying conditions, extent of response varying considerably from gene to gene Promislow (as cited by Anonymous, 2005, according to whom the paper by Promislow was due to be published in the May 2005 of the American Scientist) has studied the regulatory genes, regulating the expression of other genes. He has discovered that "the more regulators a gene has, the more plastic the gene" Smith and Kruglyak (2008) have extensively studied gene-en-vironment interaction in yeast, and have discovered "how the effects of different classes of regulatory variants are modulated by the environment" However, in these communications there is no mention of changed/ modified gene expression as becoming heritable.

(xi) Plastic behaviour of the great tit

Nussey *et al.* (2005) made observations on a Dutch population of the bird *Parus major* (the great tit). They kept in view the theoretical inference that phenotype plasticity may evolve to stability through selection. This notion has received support from some laboratory studies. The authors wanted to confirm this notion through observations on a wild population, and they chose the great tit population. They noted that in the chosen population there was plasticity with regard timing of reproduction. Some individual birds showed

mismatch between the breeding time and the time when caterpillars, which were the prey for the bird, were available in good numbers. During the period of 32 years of their study Nussey *et al.* (*loc. cit.*) noted that there was a gradual evolution of the breeding time so as to remove the mismatch. Obviously the behavioural plasticity was being replaced by fixity.

Charmantier *et al.* (2008) have studied a wild population the great tit (*Parus major*) in United Kingdom for 47 years. They noted that the individuals in the population were " markedly invariant in their response to environmental variation, suggesting that the current response may be fixed in this population" Presumably this fixity has been reached through selection, the progress of which has been observed by Nussey *et al.* (2005) in a Dutch population of this bird.

These observations are within the realm of the Synthetic Theory.

(xii) Death Valley pupfish

The Death Valley in Colorado, USA is a very dry, hot, and depressed area, 86 metres below the sea level, with temperature reaching 49° C in summer.

In the floor of the valley there are number of water bodies, large and small, isolated from each other like islands of an archipelago, and with varying environmental conditions, such as water temperature, food availability, and population density of the pupfish (*Cyprinodon nevadensis*). Populations of the pupfish in different water bodies in the valley present different phenotypes, i.e. exhibit phenotypic plasticity.

Lema (2008), with his coworkers, has studied the phenotypic variability in the pupfish.

One water body in the valley has been named as the Devil's Hole. It is 14 metres deep in a rock fissure, quite warm, and poor in food supply. The pupfishes in this water hole have small body size, large head, and flatter body. Some other water bodies, like the Big Spring, have cooler water, and with more abundant food. In such water bodies the pupfishes have a smaller head, and deeper body. Some pupfishes from the Devil's Hole were transferred to cooler waters and better food supply, and they, after only 5 years, showed smaller head and deeper body. There is an obvious relationship between environment and the structural phenotype. A behavioural plasticity has also been observed. While males, in cooler waters with better food supply, defend their reproductive territory actively and aggressively, the males in the Devil's Hole are not so active and aggressive in this respect.

The experimental studies by Lema (*loc. cit.*) and his associates show that thyroid hormone deficiency produces morphological features like those in the fishes in the Devil's Hole. The aggressive behaviour of the male fish is induced by a neurohormone, arginine vasotocin (AVT), which is secreted by some neurosecretory cells in the preoptic region of the hypothalamus. The neurosecretory cells could be identified by using an antibody to AVT. Lema and associates experimented with pupfishes from Amargosa River, reared under conditions of the Devil's Hole from the hatchling stage. The river fishes had larger neurosecretory neurons than the same sex individuals in the Big Spring with cooler water and more abundant food than the Devil's Hole. Next the Lema team injected exogenous AVT into a male from (wild population in) the Amargosa River. This resulted in the male becoming less aggressive.

Lema and his associates kept pupfishes from the Amargosa River and from the Big Spring in captivity, and have exposed them to different values of temperature and salinity. They found that the AVT systems of the fishes from the two wild populations responded differently to these environmental changes. This shows that the two populations have "evolved differences" in their proclivity to respond to these environmental variations.

Lema (*loc. cit.*) says, "Recently....accumulating evidence has established that plasticity itself has a genetic basis. Although the phenotypes generated by plasticity are induced by the environment, the phenotypic responses are produced by changes in the gene expression"

(xiii) A case of Darwin's finches

Hendry *et al.* (2008) have studied distribution of beak size in a Darwin's finch (*Geospiza fortis*) in El Garrapatero and Santa Cruz islands of the Galapagos archipelago. The distribution is bimodal, medium beak size being comparatively rare. The larger and the smaller beak sizes differ, besides in size, in the bite force capacity. This plasticity seems related to availability of small/soft and large/hard seeds. Between the two modes there seems to be some reproductive isolation, as song structure differs in birds of the two modes, and they "respond differently to each other's song" However, limited gene flow between the two modes could be inferred from analysis of DNA of microsatellites. The bimodality was being maintained in the study period due to "selective loss of birds with intermediate beak sizes" which may be due to relatively few intermediate

size seeds or to the large and small beak size birds sharing the availability of middle sized seeds.

Between 2004 and 2006 the large beak size mode was becoming taller, and the small beak mode smaller. Were the two modes on way of speciation? May be this selection in favour of the larger beak was operative during droughts, and it was not there during wet years. Besides the history of selection has been variable. "At one site (Academy Bay) bimodality was historically strong but now weak. At a second site (El Garrapatero) bimodality is currently strong. At a third site (Borrero Bay) bimodality has not been documented in the past nor the present" (Hendry *et al. loc. cit.*). Besides there are temporal fluctuations in the distribution of the two modes, and thus, a tug of war seems to be going on between the two directions of selection, or there are intraspecific evolutionary fluctuations, and thus the phenotypic plasticity in the bird species is currently being maintained.

EPIGENETIC EFFECT IN PHENOTYPIC PLASTICITY

While there is a massive support for genetic control of phenotypic plasticity, some evidence has recently surfaced inferring epigenetic involvement in this.

Epigenetics, as it is commonly understood at present, has been defined in the 'Introduction' part of this review. Waddington (1953) defined epigenesis in a different way. He regarded epigenesis as genetic assimilation of acquired characters. His concept is outdated, and has been replaced now (Bossdorf *et al.*, 2008).

Epigenesis works by the environment interfering with gene function. The interference includes "molecular forces that can activate, reduce or completely disable the activity of particular genes...." (Bossdorf *et al., loc. cit*). The changes in genes include "(i) methylation of cytosine residues in the DNA, (ii) remodelling of chromatin structure through chemical modification, in particular acetylation or methylation of histone proteins and (iii) regulatory processes mediated by small RNA molecules" (Bossdorf *et al.*). Cytosine followed by guanine or the CpG sites are in many cases clustered in regulatory regions of certain genes. Such clusters may be referred to as CpG islands. Methylation of such islands generally results in reduced activity of the associated genes. Bossdorf *et al.* opine that several types of plasticity are due to epigenesis.

Bossdorf *et al.* (*loc. cit.*) further point out that examples of epigenesis, through such environmentally

induced changes in the genome, pose a challenge to the notion that evolution occurs only through random mutations and selection. But, they say, "Yet, how serious this challenge really is we currently cannot even guess, because there is dearth of studies that addressed epigenetic questions in a real world context"

Robinson *et al.* (2008) have pointed out that social responses may be controlled by long lasting epigenetic changes in the genome. This was first noted in rats (*Rattus norvegicus*). Mother rats lick and groom their pups. If they do these motherly activities more extensively, the offspring become less responsive to stresses and more responsive to their progeny. On the other hand those rats, which have received less attention from their mother, are more easily stressed and are less responsive and less care taking to their own pups. These social responses are passed on from generation to generation. This has been found to be due to at least two epigenetic changes in DNA methylation on mother-pup extensive contacts. Thus affected DNA regions include the glucocorticoid receptor gene (which is related to formation of glucocorticoid stress hormones). In addition it includes the a1b region of DNA. Further the authors point out that upto the present epigenetic changes associated with social behaviour have been studied for only a few genetic loci, but may be more genetic loci are affected this way.

Kronauer (2008) has discussed parental imprinting of DNA in social Hymenoptera. He says that recent studies have shown that the parental imprinting occurs through DNA methylation in the honey bee and other social Hymenoptera (ants, wasps, and other bees). It has been demonstrated that in the honey bee methylation imparts information that decides whether a larva will develop into a queen or a worker. The author, however cautions that we have to await results of future empirical studies for proper interpretation of such epigenetic changes in context of the development and behaviour of these social insects.

Crespi (2008), in his review, has pointed out that the role of genomic imprinting in development of various psychotic disorders in humans has been inferred from a number of studies. It has been shown that "psychotic spectrum conditions have been mediated in part by alteration of imprinted genes in the brain" While some psychotic disorders are due to imprinted genes of maternal origin, some others are connected with imprinted genes from the male parent. Perhaps this epigenetic gene imprinting in such cases involves DNA methylation.

Leitch and Leitch (2008) have discussed genomic plasticity in polyploid plants. They point out that polyploidy results from non-disjunction of chromosomes in the germ line. Angiosperms have a remarkable capacity of tolerating the genomic impact of polyploidy, much more than in animals, including humans. Polyploid angiosperms differ in their responses to the environment, and may invade new niches. The genomic plasticity, shown by polyploid plants, may be due to a sequence rearrangement in DNA, silencing of certain sequences, and epigenetic changes through methylation.

THE BALDWIN EFFECT

In 1896 James Mark Baldwin, an American psychologist, described a new factor in evolution. Subsequently his concept came to be known as the Baldwin Effect. The Baldwin Effect, as discussed and interpreted by Crispo (2007), accepts neo-Darwinism, and the Baldwin's contribution may be taken as a supplement to the Darwinian theory. Baldwin believed that small variations in a population were not enough to address the needs arising out of a changing environment. Hence environmental changes induced new variations, on basis of which selection occurred. He referred to such selection as 'organic selection' Baldwin rejected neo-Lamarckism, as it was supported by little or no evidence.

C.H. Waddington, between 1905 and 1975, proposed a similar concept, which is often confused with the Baldwin Effect. According to Waddington changed environment produces a new phenotypic response, which through selection, gets assimilated in the genotype. As pointed out by Schlichting and Pigliucci (1993), Waddington's views were more radical and arguing for revision of the Synthetic Theory.

Waddington's views have almost no following now. Crispo (*loc. cit.*) says, "I propose that the best way to deal with this issue is to assume that Waddington misinterpreted his results, and (we) adhere to his .... genetic assimilation (concept)"

Crispo (*loc. cit.*) explains the 'genetic assimilation' of environmental effects in terms of the Baldwin Effect by taking to the principle that phenotypic plasticity may lead to more of plasticity. Let us imagine that in a certain population there is a certain range of individual phenotypic variability. If there is an environmental change or there is availability of a new niche with

somewhat different environment, and in the range of the current variability, some variant, near one of the terminals of the range, is well suited to the changed or the new environment, this variant will thrive, and, due to selection in its favour in the new environment, the favoured variant will increase in frequency, and will thus be pushing towards the middle of the range, while new mutations and cryptic variation will accumulate around it, and a new range of variation and plasticity will result. This is how 'genetic assimilation' of the effects of a new environment occurs.

Crispo (*loc. cit.*) points out that phenotypic plasticity is beneficial in two different ways, one that the plasticity allows the organism to live in a heterogeneous environment, and two that it permits the species to extend its range to new niches with novel environmental conditions, and leads to evolutionary diversification. But plasticity is eroded, if the environment is stable, and if maintenance of the plasticity is costly. this reduction in the range of variability promotes 'canalization'

The cost of maintaining polyphenism may be, for example due to :

(1) Cost of energy required for maintaining certain sensory and regulatory mechanisms,

(2) Cost of maintaining a certain phenotype needing a trade-off. For instance, the appearance of a summer morph of a pierid butterfly, with a larger thorax and greater flight capacity, is at the cost of fecundity. A summer female lays fewer eggs (Karisson, 2008).

(3) Cost of maintaining the option of different alternative developmental pathways.

Canalization' in a stable environment may be decanalized' on change of environment by concealed genetic variability finding phenotypic expression, and thus phenotypic plasticity may reappear. This situation is well illustrated in the experimental study by Suzuki and Nijhout (2006) on the black race of the tobacco hornworm (*Manduca sexta*), described under section 2, subsection (i) of this review.

Jolivet (2008) also finds neo-Darwinian interpretation of the Baldwin Effect cogent.

Nortman (?) has discussed evolution of phenotypic plasticity through the Baldwin Effect. But his predominantly anthropocentric approach, badly mixing up cultural and genetic inheritance, makes his discussion quite confusing. On one hand he rejects Lamarckism, on the other he says,"...it is not specific traits but general propensity to act in a certain (namely, more creative or intelligent) way which is reinforced and transmitted to future generations" He does not care to explain how this reinforcement occurs.

CONCLUDING REMARKS

There has been convincing demonstration of this that the phenotypic plasticity has a genetic basis. However, some evidences have recently come up showing that epigenetic modification in the expression of some genes may also contribute to the plasticity. These evidences have to be kept in view when planning future studies on the nature of the plasticity in a species, as this will help in developing a composite picture of the variability. The Baldwin Effect has served the useful purpose of drawing attention of evolutionists to the significance of environment in the evolutionary process, and of stimulating thinking about 'genetic assimilation' of the environmental effects through the neo-Darwinian mechanism.

SUMMARY

A number of illustrative studies on genetic control of polyphenism have been cited. Some recent communications, pointing to environmental factors inducing epigenetic changes in the genome, have also been referred to. The Baldwin Effect has been discussed. It has been inferred that, while the role of genome in producing phenotypic plasticity is well established, possibility of environmental epigenetic influences may also be kept in view in future investigations in this area.

REFERENCES

Anonymous, 2005. A regulatory network analysis of phenotypic plasticity in yeast; *Science Daily* April 11, 2005 (published online; http://www.sciencedaily.com/releases/2005/03/050326000025.htm).

Anthony, N.M., Johnson-Bawe, M,, Jeffery, K., Clifford, S.L., Abernethy, K.A., Tutin, C.E., Lahm, S.A., White, L.J.T., Utley, J.F., Wickings, E.J., and Bruford, M.W. 2007. The role of Pleistocene refugia and rivers in shaping gorilla genetic diversity in Central Africa; *PNAS,* **104** (Dec. 2007) : 20432-20436.

Borowski, R. 2008. Restoring sight in blind cavefishes; *Current Biology,* **18** : R23-R24.

Bossdorf, O., Richards, C.L., and Pigliucci, M. 2008. Epigenetics for ecologists; *Ecology Letters,* **11** : 106-115.

Charmantier, A., McCleery, H., Cole, L.R., Penins, C., Kruuk, L.E.B., and Sheldon, B.C. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population; *Science* no. **5877** : 800-803.

Crespi, B. 2008 Genomic imprinting in the development and evolution of psychotic spectrum conditions; *Biological Reviews,* **83** : 441-493.

Crispo, E. 2007. The Baldwin effect and genetic assimilation : revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity; *Evolution,* **61**(11) : 2469-2479.

Dahlhoff, E.P., and Rank, N.E., 2007. The role of stress proteins in responses of a montane willow leaf beetle to environmental temperature variation; *Journal of Biosciences,* **32**(3) : 477-488.

George, J. and Verma, K.K. 1994. Polymorphism in *Callosobruchus maculatus* F.–new dimensions; *Russian Entomological Journal,* **3** : 93-107.

George, J., and Verma, K.K. 1997. Variability in *Callosobruchus chinensis* L. and evolution of polymorphism in *Callosobruchus* (Coleoptera, Bruchidae); *Russian Entomological Journal,* **6** : 41-48.

George, J., and Verma, K.K. 1999. Laboratory rearing of the 'active' phase of *Callosobruchus maculatus* F. (Coleoptera, Bruchidae); *Indian Journal of Experimental Biology,* **37** : 584-588.

Hendry, A.P., Huber, S.K., De, Leon, L.F., Harrel, A., and Podos, J. 2008. Disruptive selection in a bimodal population of Darwin's finches; *Proceedings of the Royal Society, B* (published online, doi: 10.1098/rspb.2008.1321).

Jeannel, R. 1950. *La Marche de l'Evolution* (Paris, Editions du Museum)

Jolivet, P. 2008. Baldwin Effect and phenotypic plasticity; *XXth International Congress of Zoology, 26th to 29th August, 2008, Paris.*

Karisson, B. 2008. Seasonal polyphenism and developmental trade-off between flight ability and egg laying in a pierid butterfly; *Proceedings of the Royal Society, B: Biological Sciences,* **275** (Sept. 22, 2008) 18522912 (P,S,E,D).

Kronauer, D.J.C. 2008. Genomic imprinting and kinship in the social Hymenoptera; *Journal of Theoretical Biology,* **254** : 737-740.

Kronfrost, M.R., and Gilbert, L.E. 2007. The population genetics of mimetic diversity in *Heliconius* butterflies; *Proceedings of the Royal Society, B* (published online, doi:10.1098/rspb.2007.1378).

Leitch, A.R. and Leitch, I.J. 2008. Genomic plasticity and the diversity of polyploidy plants; *Science* **320** 481-483.

Lema, S.C. 2008. The phenotypic plasticity of Death Valley pupfish; *American Scientist,* **96** : 28-36.

Lemos, B., Araripa, L.O., and Harti, D.L. 2008. Polymorphic Y chromosomes harbor cryptic variation with manifold functional consequences.; *Science,* **319** : 91-93.

Niven, J.E. 2008. Evolution: convergent eye losses in fishy circumstances; *Current Biology,* **18** : R27-R29.

Nortman, D. (?) The evolution of phenotypic plasticity through the Baldwin Effect; *Philosophy Noesis,* VI, Article 4. Published online, http://www.chass.utoronto.ca/pcu/noesis/issue_vi/noesis_vi_4.html (downloaded on 10th July 2008).

Nussey, D.H., Postma, E., Gienapp, P., and Visser, M.E. 2005. Selection on heritable phenotypic plasticity in a wild bird population; *Science,* **310**(5746) : 304-306.

Robinson, G.E., Fernald, R.D., and Clayton, D.F. 2008. Genes and social behaviour; *Science,* **322** : 896-900.

Schlichting, C.D., and Pigliucci, M. 1983. *Phenotypic evolution: a reaction norm perspective* (Sunderland, MA, Sinauer Associates).

Schilthuizen, M., Craze, P.G., Cabanban, A.S., Davison, A., Stone, J., Gittenberger, E., and Scott. B.J. 2007. Sexual selection maintains whole-body chiral dimorphism in snails; *Journal Compilation (European Society for Evolutionary Biology)* (online, doi: 10.1111/j.1420-9101.2007.01370.x).

Smith, E.N., and Kruglyak, L. 2008. Gene-environment interaction in yeast gene expression; *PLoS Biol.,* **6**(4) : e83 (p.-810-824).

Suzuki, Y., and Nijhout. F. 2006. Evolution of polyphenism by genetic accommodation; *Science,* **311** : 650-652.

Tiwary, P.N., and Verma, K.K. 1989a Studies on polymorphism in *Callosobruchus analis* (Coleoptera, Bruchidae). Part I–characteristics of phases; *Entomography,* **6** : 269-290.