Genetic
Geophysical and ~~Tectonic~~ Causes of the Periodicity of Evolution

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Introduction

Recent estimates of allozyme variation in natural populations and the rates of molecular evolution (clock mode) raise several special problems which, I think, are related to general understanding of the meaning of evolution. To Darwin the organic evolution was an inevitable consequence of, in his words, organism to organism relations, i.e. variation and competition, while his catastrophic-thinking opponents believed in long periods of quiescence interrupted by sudden changes under exceptional circumstances. Darwinians obtained their evidence from comparative morphology and stressed variation whereas catastrophists relied on fossil record and adhered to typological concept. The Darwinian theory was subsequently adopted by paleontologists who nevertheless believed in causal relations between major evolutionary and geological events which "stimulate the sluggish evolutionary stream to quickened movement". These phrase of R.S.Lull had been frequently quoted until it was severely criticized by G.G.Simpson and other authors. Within the classical genetics, there have been also two schools, one confiding in permanent small mutations and the other prefering occasional macromutations. The first school apparently profited from modern studies of allozyme polymorphisms showing a large amount of genetic variability in populations of many species. However, the evolutionary consequences of genetic polymorphisms are disputable and some molecular biologists have challenged the canonical concept of Darwinian evolution (Kimura,1968; Kimura and Ohta,1971,1973; King and Jukes,1969 and the criticism of these works in Clarke, 1970, 1973; Wills,1973; Ayala and Gilpin,1973; Ayala et al., 1974; Lewontin,1973; Selander and Johnson,1973, etc.).

One can suppose that the meaning of evolution would emerge from comprehensive evolutionary synthesis, and as an attempt of such a synthesis in a short paper is futile. I would only summarize those hypotheses which I believe to be the most promising for the future synthesis.

Potential polymorphism

The potential variability is often perceived as practically unlimited, i.e. when particular mutation is needed it would not keep us waiting too long. The electrophoretic technique has revealed high but by no means unlimited genetic variability. It is rather striking that an average heterozygosity is much the same in Drosophila, rodents, and man (see Lewontin,1973; Selander and Johnson.1973). Johnson (1972,1973) has shown that equitability of allele frequencies is greater for loci with higher numbers of alleles. He used this as an evidence against selective neutrality of polymorphism. I think, however, that other explanations are possible. The equitability of allele frequencies in highly polymorphic loci may indicate that these loci are saturated, i.e. close to the limit of potential polymorphism allowed by a given genetic system under relaxed selection control. Less polymorphic loci are kept by selection well under their saturation state, and as selection pressure varies they display variable allele frequencies. Further evidence for restricted number of definite allelic states come from Vavilov's (1922) law of "homologous series in variation" (or similarity in allelic va - riation at homologous loci in related species) supported by compelling examples. The meaning of this law apparently is that similar genetic systems of related species allow the same alleles at majority of homologous loci. Rapid restoration of polymorphism was observed in laboratory populations founded with a few individuals. The restored allele frequencies were much the same as in a source population.

Much debated question of whether many polymorphisms are selectively advantageous or neutral can be approached from somewhat different point of view. It is well known that rudimentary organs which have lost their function (i.e. selectively neutral) are the most variable. Many studies of morphogenic correlations have shown that more tightly correlated characters are more variable and vice

versa (Kolosova, 1975). The explanation is that in the case of constant characters the morphogenic correlations are loosened by stabilizing selection. Thus, the stronger is selection pressure the less variable are morphological characters. It appears that the same is true at molecular level.

Most polymorphisms show centrifugal geographical pattern, i.e. they are at maximum in central populations and decrease toward more exacting marginal environments (see Soulé,1973). This applies especially to the inversional polymorphism but also to at least several well studied cases of morphological and allozymic variation (e.g. Nevo, 1973). According to Goodman and Moore (1973) the initially high mutation rates at hemoglobin loci have been eventually declarated but are still kept high at loci with unknown function.

There is also some indirect evidence. Electrophoretic studies have demonstrated high level of genetic polymorphism in stable (tropical, deep-sea) environments and comparatively low variability in unstable environments (Ayala and Valentine,1974). It is assumed that stabilizing selection (chiefly in the form of r-selection) is weaker in stable environments. This evidence contradicts experimental results of Beardmore (1970), Powell (1971) and other authors (see Gillespie and Langley,1974) who claim positive correlation between allozymic variation and environmental instability, but attempts on modeling stable or unstable environments in a cage appear somewhat inadequate and the results are rather ambiguous (Soulé, 1973).

To summarize, each genetic system exhibits a certain amount of potential polymorphism, i.e. a limited number of definite alleles which would apply in abstract situation when natural selection is completely removed. This allelic swarm is moulded by natural selection so that at many loci the observed variation differs considerably from its potential polymorphism. The changes in selection pressure not only alter the frequencies of alleles but also reveal some previously suppressed parts of potential variability which appear as new mutations. Under relaxed selection, the observed poly - morphism approaches its potential level. Thus, a level of polymorphism is negatively correlated with selection pressure and high polymorphism are not necessarily advantageous or maintained by heterotic selection. At this point the present hypothesis agrees with that of selective neutrality. However, all observed polymorphisms are pre-

sumed to be sensitiv to selection and the random drift is but of minor significance in distribution of allelic frequencies.

Microevolution versus megaevolution

The genetic distances between semispecies and between subspecies are much the same (Ayala et al.,1974). This suggests that a few genes may be involved in reproductive isolation (Dobzhansky, 1974) and that the multiplication of species (speciation or microevolution) is not necessarily accompanied by evolutionary innovations. On the other hand, the evolutionary novelties can hardly be achieved by occasional advantageous mutations because any mutations alien to a given genetic system are highly improbable. They arise in response to general changes of genetic system, i.e. macromutations.

Goldschmidt (1940) has conceived macromutations chiefly as the changes of relative growth rates. This kind of macromutations may be illustrated by paedogenic mutations which are claimed by Garstang (1928), De Beer (1951), Romer (1972), Takhtadzhian (1973), Bolk (1926) and other authors to be responsible for appearance of vertebrates, angiosperms and even man. But many evolutionists which have not adopted the concept of paedogenesis would also agree that more subtle changes of morphogenic correlations are of great evolutionary consequence (e.g.Mayr,1960).

The problem of morphogenic control is far from settled but at least some controlling factors are proved to be equally impor - tant for both unicellular, and multicellular organisms. These are morphogenic "reference points" (Wolpert,1969,1971; Sonneborn,1974, etc.) and critical distances between, e.g. Paramecium oral structures (Sonneborn,1974) or vertebrate dentition (Osborn,1974; see also Vermij,1973 and references cited there) imposed by inhibition gradients. These morphogenic processes depend upon interaction of a gene with products of other genes of the same or other cells acting as inducers or repressors of forming receptor hormone - histone complexes (Kolata,1974; Stein et al.,1974).

However, Hanson and Kaneda (1968) presented evidence of intranuclear control of sequential activity in a single cell (in Paramecium) which is independent of any cytoplasmic events. They

postulated not only intercellular but also intracellular control of differential gene activity within multicellular systems. Sequential order of some morphogenic events is amazingly persistent (e.g. the development of reproductive glands at the same age in apes and man : De Beer,1951) which also points to highly autonomous controlling mechanisms.

In Saccharomyces, there are indications of centromeric heterochromatin control of sequential gene activity (Tauro et al.,1968; Mortimer and Hawthorne,1973). According to Prunel and Bernardi(1974) model, the petite mutations affecting the growth rates of the yeast cells are caused by deletions in spacers (i.e.,the AT rich regions) of mitochondrial genomes. A gradient of renaturation rates of AT rich repetative units is correlated with the replication chronology and transcription activity (Tupitsina et al.,1974). Thus, repetative sequences which are the entry sites for RNA polymerase (Dickson et al.,) may function as sequential controlling mechanism.

In multicellular organisms, the highly repetative DNA is mostly organized in blocks of eentromeric heterochromatin, while intermediate repetative sequences are dispersed along the genome and there is at least one repetative region per unique sequence. Con - sidering the abundancy (up to 80%) of this class of repetative units in higher organisms one can suppose that their functions are expanded from controlling the time of gene expression in the cell cycle to ordering a sequence of morphogenic events through the life cycle of multicellular system. Fidelity of control is probably provided by rebundancy of repeated sequences. Mutagenic and paramutagenic effect of variations in intermediate repetative DNA redundancy (e. g., the redundancy of rDNA) was demonstrated in both plants and animals (Brink,1973 ; Phillips,1974, etc.). It is of prime importance that redundancy variations are dosage-sensitive, e.g. deletions in bobbed locus of Drosophila are compensated by sudden reproducible increase in rDNA redundancy (Tartof,1973; Graziani et al.,1973). One can suppose that dosage-sensitive changes in DNA redundancy may be induced also by increased metabolic activity of certain genes which is evindenced, e.g. by higher RNA to DNA ration in brain cells of "enriched" (living in complex environment) rats (see Wallace, 1974). Kazakhashvili (1974) has observed similar increase in RNA contents in the rat hippocampal neuron cells under intense training. This may explain how DNA redundancy can be affected by radical chan-

ges in ecology causing acceleration or deceleration of morphogenic trends.

Rates of evolution in different selective environments

The above hypothesis assumes intimate relations between evolution of a genetic system and ecological innovations which result from and contribute to ecosystem evolution.

The history of ecosystems is inscribed in the fossil record. Stratigraphic scale can be viewed as a sequence of paleoecosystems and the boundaries of major stratigraphic units are marked by re - placements of dominant types which occurred simultaneously among plants and animals. For example, in the mid-Cretaceous, the angiosperms replaced cycadophyted in the undergrowth (Krassilov,1972) while mammals achieved dominance among small vertebrates (Bakker, 1971). Similar replacement among the forest canopy trees and large vertebrates was postponed for the Paleocene time.

It was suggested that morphological complexity of dominant types matched functional complexity of their ecosystems (Suschkin, 1922). Though many species became extinct at paleoecosystem boundaries, their adaptations not necessarily vanished with them. More often these adaptations have been retained by replacing species which have added to them some new adaptations. Hence ecological structure of biotic communities gained in complexity causing progressive complication of their dominant types (Krassilov,1973a). This complication trend was conveyed in Haeckel's "ages" of fishes, reptiles and mammals, while J.Huxley (1955) conceived biological pro - gress as replacement of dominant types. However, this process was not unidirectional. Mesozoic dominant types - conifers, cycadophytes and ginkgophytes among plants and dinosaurs among animals were less advanced in terms of approaching angiospermous and mammalian level of organization than their $P_a$leozoic predecessors - pteridosperms and therapsids. This Mesozoic twist of evolution probably resulted from different structural complexity of corresponding ecosystems (Krassilov, 1973b).

The complexity of ecosystem is negatively correlated with the niche sizes. Ramensky (1914) distinguished between "explerents" pioneering early stages of succession and "violents" dominating climax ecosystems. In modern terms, the explerent are r-selected and

the violents are K-selected. Not only successional stages but also climax ecosystems thriving under different environmental regime differ in explerents to violents proportions. Vilentine (1971) suggested that the course of evolution had been much affected by prevalence of their K-selection or r-selection. In stable environments, K-selection promoted specialization while generalized populations were favoured by r-selection in unstable environments (see also Frerichs, 1971).

According to Bretzky and Lorenz (1970) model, the rates of evolution and extinction are higher in stable than in unstable environments. This model provoked much controversy in paleoecological literature (Eldredge,1974; Rohr and Boucot,1974; Levinton,1974,etc). It is necessary, as discussed above, to distinguish between speciation and megaevolution, for speciation may proceed within the limits of potential polymorphism of a genetic system and without any genuine innovation while megaevolution depends on macromutational changes of genetic system. Species diversity is higher in stable environ - ments and the rates of speciation are presumably also higher but this is not necessarily so for megaevolution. In general, the corre- lation between diversity and the rates of evolution appears to be ne- gative. Large genera with many species (such as Drosophila with about 1200 species) are as a rule more conservative than small gene- ra. The same is true for separate organs, e.g.,the leaves of early angiosperms were much more diverse and variable than their reproduc- tive structures, but they remained much the same from the Cretace - ous time to present while flowers, fruits, and pollen grains under- went radical changes (Krassilov,1973c). The hypotheses of tropical origin of many higher taxa assuming higher rates of megaevolution in stable environments are based on tropical distributions of less ad- vanced members of these taxa at present and on unwarranted assump - tion that relics are preserved at the same environment which gave rise to their more successful relatives. The flowering plants are among those groups for which the tropical origin is favoured by majo- rity of recent authors. However, the most acceptable ancestors of these plants occurred in the fossil plant assemblages of the Late Mesozoic temperate zone and the angiospermization was probably pro- moted by seasonal climate (Krassilov, 1975a).

Selection for reproductive rates (i.e. r-selection) would affect also growth rates. If megaevolution depends chiefly on chan-

ges in relative growth rates as discussed above, then the rates of
megaevolution would be higher under r-selection in unstable environ-
ment. As environmental instability increases, the diversity decreases
and some populations become extinct. The surviving populations under-
go changes analogous to those in marginal populations as compared
with the central ones, i.e. their genetic polymorphism is reduced
and they experience ecological shifts. This may be illustrated by in-
crease in draught resistance in a sequence of homoselected Clarkia
populations under so called "catastrophic selection" (Lewis,1962;
Bartholomew et al., 1973).

Periodicity of evolution and molecular clock model

Any environmental factor disturbing the ecosystem climax would
thus promote the megaevolution via macromutations in homoselected po-
pulations, while stabilizing trend would be coupled with vigorous
speciation. These theoretical expectations are supported by correla-
tion of major megaevolutionary episodes with tectonic and climatic
events. For example, the earliest Metazoan fauna appears in North
America, Europe, and northern Africa just above the "Laplandian"til-
lites evidencing the widespread glaciation about 68 my BP (Sokolov,
1974). The appearance of chordates is correlated with the Late Ordo-
vician glaciation (Harland,1972; Havlíček,1974). Major progressive
steps in the evolution of terrestrial ecosystems were (I) 370 my BP,
Givetian (Middle Devonian) time : the appearance of progymnosperm
forests with earliest insects and labyrinthodonts, (2) 325 my BP, Na-
murian or early Pensylvanian time : the appearance of mesophytic de-
cidious forests - Angara and Glossopteris floras - in both northern
and southern hemispheres, (3) about 230 my BP, Late Permian - Early
Triassic time : the rise of therapsid faunas, (4) 100-90 my BP, mid-
Cretaceous time : the rise of angiosperms and small mammals, (5) 65
my BP, Danian : replacement of dominant types after the mass extinc-
tions in the terminal Cretaceous, (6) 26 my BP, Miocene : the expan-
sion of steppe biome. Step (I) was correlated with major Devonian
compressional phase which was assigned to Eifelian (about 380 my BP)
in the western North America (Boucot et al., 1974) and to Givetian
in the Ural fold belt and Western Europe, and also with the spread-
ing of seasonal summer-dry climate evindenced by the red beds. Step
(2) was associated with compressional episodes in the Alleghenian,

Hercynian, Mongolo-Okhotian fold belts and elsewhere, and with the onset of Gondwana glaciation. Step (3) occurred during the restoration of Pangaea and the red bed climate, while the (4-6) coincided with compressional phases (especially evident in the Tethys area), the cooling episodes in the mid-and terminal Cretaceous (Krassilov, 1975b), and the increased aridity in the Miocene.

The Mesozoic climatic pessima fall on the beginning and the optima on the latter half of each epoch (Krassilov, 1973d, 1975b). The Mesozoic epochs, thus, correspond to climatic cycles and, I think, the same is true for Paleozoic and Cenozoic epochs.

In general, the periodicity of megaevolution corresponds to tectonic and climatic cycles which are interrelated and mutually depend on the changes in the earth rotational regime (Steiner, 1967; Williams, 1972; Krassilov, 1974a). Valentine and Moores (1972) have suggested unstable shelf environments under compressional regime (when the continents collided). It appears that climatic deterioration and the prevalence of seasonal climates during compressional phases also contributed to environmental instability. That is why the boundaries of the global biostratigraphic units are controlled chiefly by climatic changes and the hierarchy of these units roughly corresponds to the hierarchy of climatic cycles (Van der Hammen,1961; Krassilov, 1974b).

Periodicity of organic evolution imposed by climatic cycles is consistent with recent estimations of mutation rates in protein molecules. It was claimed that the rate of substitutional process is uniform in different parts of the phylogenetic tree. The constancy of substitution rates, i.e. the molecular clock model of protein evolution was coupled with neutral hypothesis of protein polymorphism. However, Johnson (1973) suggested that the rates of protein evolution might convey the rate of change in selective environment. More detailed reconstructions of protein phylogenies (Goodman and Moore,1973) have shown not uniform but, in fact, periodically fluctuating rates of molecular evolution. One can assume high initial rates after macromutational event and subsequent deceleration while the genetic system is approaching the limit of its potential poly - morphism.

Summary

It is suggested that each genetic system allows certain amount of allelic variation at a locus which constitutes its potential polymorphism. In stable environment, the genetic variability increases up to its potential level and the high rate speciation within the limits of potential polymorphism is promoted by K-selection. Speciation is decelerated while an ecosystem approaches its climax state. New cycle of evolution is triggered by tectonic and climatic events which disturb the climax and reduce diversity causing extinctions as well as instability (ecological marginality) of surviving homoselected populations. Megaevolution in these populations results from the changes of growth rates under strong- r-selection. A sequence of morphogenic events may be affected by ecological shifts via macromutational changes in DNA redundancy in response to increased metabolic activity of certain genes. New genetic system reveals its microevolutionary potentials on the way to new ecological homeostasis. Thus, evolution is periodical and this is reflected by the changes of substitution rates in protein molecules.

A synthesis of evolutionary events at molecular, morphological and ecosystem levels is necessary for a comprehensive theory of evolution. It must be admitted that the hypotheses linking these events remain more or less speculative. This paper is a plea for broader outlook on special problems arising in the different departments of evolutionary biology.

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