M. Feldman

Evolutionary Processes and Theory: Micro- and Macroevolution

Eviatar NEVO

Institute of Evolution, University of Haifa, Mt. Carmel, Haifa 31905, Israel

Is a new evolutionary synthesis necessary? The problems of tempo and genetic revolution in speciation and the relationship between micro- and macroevolution are reviewed. Evidence from the active speciation of subterranean mole rats of the *Spalax ehrenbergi* superspecies in Israel, and the *Spalax leucodon* superspecies from Turkey is overviewed. Likewise, inter- and intraspecific evidence is reviewed on genetic diversity in nature from local, regional and global earlier analyses of numerous taxa. It is concluded that genetic revolutions, punctuations, and stasis are not the hallmarks of speciation. Speciation can encompass all tempos from gradual to punctuational and is usually not based on genetic revolutions. Macroevolutionary processes are underlain by microevolutionary processes. The evidence suggests that qualitatively new mechanisms are unnecessary to account for macroevolutionary patterns. The synthetic Theory of Evolution is strongly supported by the available molecular and organismal evidence and is only enriched by it. Future studies at the molecular level are expected to bridge between micro- and macroevolution and between molecular and organismal biology.

The Evolutionary Process

COSMIC EVOLUTION

The most fundamental process in the Universe and on our Planet is evolutionary change. This process has been highlighted by all sciences in the all-embracing theory of Cosmic Evolution, which comprises physical, chemical, biological and human interlinked stages of evolution (Nevo, 1995a). The universe is not static, small and young, as was conceived by prescientific world beliefs. In contrast, science indicates that the universe is large, old, evolving and ever-dynamic. The major discovery of the human brain is that the universe and its components, that is, time, space, matter, galaxies, stars, planets, life and humans themselves are interrelated historical entities that are constantly evolving.

The basic features of nature comprise change and evolution from simple to complex physical (Weinberg, 1977; Davies, 1988; Hawking, 1988) and biological (Kauffman, 1993) entities, from chaos to antichaos, or increasing order and complexity. The climax of this

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evolutionary process on our planet (and probably on other numerous planetary systems in the universe, circling stars in thousands of billions of galaxies) is the astounding evolution of biodiversity and the extraordinary complexity of neural systems, as is exemplified locally on our planet in the human brain. The evolutionary theory of the universe relates energy matter and life into a consistent comprehensive theoretical and lawful framework presumably beginning with the astronomical Big Bang explosion, 15±4 billion years ago (Ba). Our own solar system, which evolved around 4.6 Ba, set the stage for the evolution of life, biodiversity and human culture (Stanley, 1986).

Biological evolution is characterized by transitional stages from inorganic to organic matter, the origins of life, prokaryotes, the genetic code, eukaryotes, meiotic sex, multicellularity, biodiversity, social and cultural evolution (Maynard-Smith and Szathmary, 1995).

Biological Evolution

Life originated about 4 billion years ago from a primitive common ancestor (Margulis, 1982; Stanley, 1986; Maynard-Smith and Szathmary, 1995). All biodiversity was generated gradually through the Darwinian mechanism of natural selection (Darwin, 1859). Recently, an attempt has been made to consider Darwinism in a broader context of the origin of spontaneous order that is, the evolution from simple to complex systems that can exhibit powerful self-organization (Kauffman, 1993). Clearly, such spontaneous order is available to natural selection (or to random drift) for the further selection of design. Most life experiments (i.e., billions of biological species) became extinct by background or massive extinctions (Chaloner and Hallam, 1989; Raup and Jablonsky, 1986; Donovan, 1989; Nevo, 1995a). Nevertheless, regardless of all extinctions, the history of global biodiversity over evolutionary time is of increasing diversity to the present all-time high (Wilson and Peter, 1988).

The catalogued number of species is between 1.5-1.8 million, but the true number is yet unknown and may range from 10-100 million species. Most of these derive from the tropical rainforest canopy (May, 1988; Erwin, 1988; Ehrlich and Wilson, 1992).

The Problems

MODE, TEMPO AND PATTERNS OF BIOLOGICAL EVOLUTION

Biodiversity increased through the origination of new species in two possible ways: cladogenesis (i.e., splitting or fragmentation of populations into reproductively isolated and ecologically compatible species in space), or anagenesis (i.e., gradual phyletic evolution over time) (Simpson 1944, 1953; Mayr, 1976; Grant, 1991). Despite the heated debates on the tempo and mode of speciation in nature, whether primarily cladogenetic (Eldredge and Gould, 1972) or anagenetic (Rensch, 1959), no reliable estimates exist on the relative importance of either mode or tempo of evolution, over time, space, and across different phylogenetic groups. At any rate, the problem is by nature quantitative rather than qualitative, and we need to determine, therefore, how much of each takes place.

To take one example only, in thorough and in-depth analysis of arvicolid rodents, Chaline (1987) found the following interesting quantitative results. The arvicolid radiation generated 140 lineages, 98 of which are still living. These 140 lineages, distributed within 37 distinct genera, involved at least 140 speciations. Paleontologically, 38 of the 140 lineages are well documented (27%), whereas 103 lineages (73%) are not. Yet, Arvicollidae represent one of the best-known groups. Phyletic gradualism through anagenesis contributed 39% of Eurasian arvicolid evolution, whereas allopatric speciation through cladogenesis contributed only 35%, and stasis attained a maximum of 26%. The arvicolid data suggests that anagenesis and cladogenesis can no longer be considered as the two major evolutionary modes. They are patterns resulting from various modes of speciation (spatial, temporal and populational).

The arvicolid data leads to rejection of the punctuated equilibrium model (Eldredge and Gould, 1972; Gould and Eldredge, 1977, 1986, 1993) that confuses between modes and processes. This model had launched a false controversy, setting biological against paleontological data, when in fact they are complementary (Chaline, 1987). Mole rats, spalacids (Nevo, 1991) and subterranean mammals (Nevo, 1979, 1995b) also generally corroborate evolutionary gradualism in space and over time). Emphatically then, the problem of modes and tempo in evolution is strictly quantitative: how much of each?

Genetic Revolutions in Speciation

Is the arvicolid case exceptional or does it represent the general rule? Are new species formed abruptly, in rare catastrophies, distinct from the normal process of phyletic evolution? Or does reproductive isolation evolve gradually, as a by product of the divergence of gene pools? The idea that species evolve by genetic revolutions through founder effects has been advocated by Mayr (1954, 1963, 1970, 1976, 1982), Dobzhansky (1937, 1955, 1970) and others (e.g., in Giddings et al., 1989). Presumably, an isolated population, small in numbers and in geographic extent, colonizes a new area. Changes in selection pressures and genetic drift result in the rapid shift of many genes to a new, coadapted gene combination, which is reproductively isolated from the ancestral population. Carson (1968, 1970, 1975, 1982) and Templeton (1979, 1980a,b,c, 1981, 1982a,b), among others, have suggested similar models and advanced arguments for the founder flush-crash version of the theory (Carson and Templeton 1984). This stimulated a number of experimental tests yielding inconsistent results (Powell, 1978; Dodd and Powell, 1985; Ringo et al., 1985, 1986, 1987a,b; Meffert and Bryant, 1991, 1992, 1993; Galiana et al., 1989, 1993; all cited in Moya et al., 1995). A 10-year-long and large-scale experiment with *Drosophila pseudoobscura*, designed to test the founder effect theory of speciation, failed to corroborate it (Moya et al., 1995). Theoretical arguments have been also raised against the founder-effect theory of speciation (Barton and Charlesworth, 1984; Rice and Hostert, 1993; Rouhani and Barton, 1987; Barton, 1989; Coyne, 1990; Charlesworth, 1991; Coyne, 1994 - all cited in Moya et al., 1995).

The advance of molecular genetics suggested that speciation does not necessarily comprise genetic revolutions (Nevo and Shaw, 1972; Nevo and Cleve, 1978; Ayala, 1975). In fact, the studies of subterranean mole rats, the Spalacidae, suggested that speciation may occur with minor alterations in structural and/or regulatory genes, as well as with chromosomal evolution (Nevo, 1985, 1991; Nevo and Cleve, 1978). Criticisms of the founder effect genetic revolution model of speciation have been advanced by Wright (1978) and Lande (1980). Barton and Charlesworth (1984) also theoretically criticized the founder effect models, and brought empirical evidence that denies support for a major role for founder effects in speciation. Theoretical models of founder effect speciation show that under a wide variety of assumptions, the probability that a founder population will undergo a stochastic transition to a new selective equilibrium, causing significant reproductive isolation from its ancestral population, is low (Barton and Charlesworth, 1984).

Empirical evidence from peripheral desert mole rat populations of the *Spalax ehrenbergi* superspecies (Nevo, 1989, 1991) indeed supports the idea that genetic polymorphisms in the isolates are retained, and may be even higher than in populations of the main range, though similar in their genetic profile (Nevo, 1989). Furthermore, these high levels of genetic polymorphisms are explicable by natural selection (Nevo et al., 1996). The data on *S. ehrenbergi*, (Nevo, 1989; Nevo et al., 1996) and other evidence (e.g. Nevo et al., 1974, Mewaldt, 1982), indicate that appreciable polymorphism can be preserved in small size populations.

Current theoretical models predict fast gene fixation in small populations without mutation or gene inflow. Using multilocus modelling, we demonstrated that strong selection for traits controlled by additive genes could oppose random fixation in small panmictic populations during thousands of generations. The common feature of the polymorphic trajectories in these models is the formation of strong linkage disequilibria with very few prevailing haplotypes that represent the entire multilocus variation in the population at any moment (Nevo et al., 1996; see also Lande, 1980).

Even if genetic drift is not a consequence of small size population effects, isolates could still provide speciation cradles. Rapid chromosomal speciation may generate initial postzygotic reproductive isolation in the small isolate (i.e., by Robertsonian mutations, White, 1978). Premating reproductive isolation can increase gradually over time, thereby providing sufficient reproductive barriers from the ancestor and the potential to advance into ecologically open niches. If so, then peripatric speciation can occur though without genetic revolution (Nevo, 1991). There is a broad correlation between rates of speciation and chromosomal evolution. This led to the suggestion that random fixation of chromosome rearrangement in small populations plays an important causal role in speciation (Bush et al., 1977; Levin and Wilson, 1976; White, 1978). Alternative interpretations can be proposed, however (e.g., Lande, 1979; Bengtsson, 1980; and Charlesworth et al., 1982).

The Molecular Basis of Speciation

The introduction of molecular genetic techniques, initially of protein polymorphisms during the 70's, has enabled the quantification of the amount of genetic divergence among populations, reproductively isolated or not (Nevo and Shaw, 1972; Nevo and Cleve, 1978; Lewontin, 1974; Ayala, 1975, 1976; Avise and Ayala, 1975; Nei et al., 1975; Avise, 1976; Avise and Aquadro, 1982). These early studies indicated the following results: (i) The development of reproductive isolation per se may not require many gene changes; (ii) The process of speciation might be completed with relatively few additional gene changes. The two emerging daughter species might remain quite similar at the single gene level, though the final termination of gene exchange and the elimination of fertile hybrids in narrow hybrid zones might be a gradual and lengthy process, like in *Spalax*, in contrast to the rapid emergence of reproductive isolation (Nevo, 1991). (iii) Genetic distances between populations and species (=D, Nei, 1972) vary manyfold among taxa, based on 3800 genetic distances between pairs of vertebrate species (Avise and Aquadro, 1982). For example, avian congeners are extremely conservative in magnitude of protein divergence relative to all amphibian congeners. Fish and mammalian genera are highly variable in *D*, but generally are intermediate in level of divergence to the birds and amphibians.

From the early molecular studies of proteins it became abundantly clear that species vary in kind, in accord with different strategies of evolutionary adaptations and speciation patterns (Nevo and Cleve, 1978). Reproductive isolation may either follow or precede the genic or chromosomal divergence of gene pools, and so speciation may be associated with either major or minor alterations in structural and/or regulatory genes, as well as with chromosomal evolution. The extent of genetic differentiation depends on various correlated and interacting factors, including the taxon, mode and rate of speciation; population and migration size and structure; breeding and mating system; reproductive strategy; chromosomal rearrangements and polyploidy; and the ecological selection structure.

To become both predictive and falsifiable, speciation theory must be based on critical multifactorial tests incorporating the genetic system, the ecological regime and historical patterns in actively speciating populations (Nevo and Cleve, 1978). Likewise, it has been suggested that genetic differentiation is a function of time and is not correlated with rates of speciation, though it is proportional to the number of speciation events in the group (Avise and Ayala, 1975). Further testing of this model is required, particularly with the immense newly accumulated data of protein and DNA sequences in databases. Notably, however, the evidence available in databases has not been collected with the problems of speciation, micro- and macroevolution in mind, and hence suffers an obvious limitation (see below).

The revolution in molecular biology introduced DNA polymorphisms into the attempt to quantify speciation (e.g. Wallace, 1963; Ohno, 1970; Stebbins, 1969; Britten and Davidson, 1969; Selander and Johnson, 1973; Wilson et al., 1977; Nevo, 1990, 1993). White (1978) advocated the major role played by structural chromosomal rearrangements in initiating speciation. Additional discoveries about DNA (e.g. repetitive DNA, mitochondrial DNA, and transposable elements) and about mechanisms of DNA change (e.g., gene conversion) led to their suggested involvement in speciation (e.g., Schopf, 1981; Milkman, 1982; Avise et al., 1983). Recent studies in speciation have shown that reproductive isolation between the young emerging *Drosophila* species is not polygenic, but rather is based on a few major speciation genes that affect hybrid fitness (Coyne, 1992; Orr, 1993). Likewise, mating discrimination and the sterility or inviability of hybrids increase gradually with time (Coyne & Orr, 1989). This is also true in *Spalax* (Nevo, 1985, 1991).

The Dilemma of Micro- and Macroevolution: Can Microevolution Account for Macroevolution?

Is there evidence to support the claim that the genetic variation between species differs qualitatively from that of variation between populations of the same species, or from that between individuals of the same populations? Can microevolutionary mechanisms and processes operating *within* species be extrapolated to explain macroevolutionary differences *among* species and higher taxa? This major recurring problem has been extensively debated in evolutionary biology (e.g., Haldane, 1932; Dobzhansky, 1937, 1941, 1951; Simpson, 1944, 1953; Mayr, 1954, 1963, 1982; Goldschmidt, 1940; Stebbins, 1950, 1974; Rensch, 1959; Eldredge and Gould, 1972; Charlesworth et al. 1982; Stebbins and Ayala, 1981; Hecht and Hoffman, 1986; Avise et al., 1987; Levinton, 1988; Grant, 1991).

Can the microevolutionary processes operating within populations (e.g., mutation, recombination, migration, genetic drift and natural selection) account by themselves for macroevolutionary phenomena and can they predict macroevolutionary patterns? Do microevolutionary processes operate at present, and did they operate in the past, across taxa in which macroevolutionary phenomena are observed? Is the Darwinian view that evolution proceeds by natural selection (i.e., converting variation among individuals within interbreeding populations into variation between populations in space and time) valid at higher hierarchical levels? In other words, does microevolution extend gradually and naturally into macroevolution, or should additional kinds of genetic processes be postulated to explain macroevolutionary patterns and processes? The dichotomy is substantial between those who claim that macroevolution is a continuous extension of microevolution (Darwin, 1859; Fisher, 1930; Haldane, 1932; Wright, 1940; Mayr, 1942, 1963; Simpson, 1944, 1953; Stebbins, 1950, 1974; Charlesworth et al., 1982; Avise et al., 1987; Hoffman, 1989; Grant, 1991; Nevo, 1991, 1995a) and those who consider them different phenomena (Goldschmidt, 1940; advocates of the "punctuated equilibria" theory of evolution, e.g. Eldredge and Gould, 1972; Gould and Eldredge, 1977, 1986, 1993; Gould, 1980, 1982a,b; Stanley 1975, 1979).

Is a New Evolutionary Synthesis Necessary?

For Gould (1980), evolutionary theory, "as a general proposition, is effectively dead, despite its persistence as a textbook orthodoxy". Punctuationists assert that the predominant pattern in the fossil record of most taxa is the rapid burst of change followed by the stasis of established species, with most morphological change occurring quickly on a geologic time scale during speciation. Morphological stasis of most lineages and the sudden appearance ("punctuation") of new forms is contrasted with the alternative Darwinian mode of gradual evolution of species. Furthermore, some punctuationists argue that the pattern in the fossil record is inconsistent with predictions made by the Synthetic Theory of Evolution that evolution, when viewed on a geological time scale, is slow and gradual.

More than 50 years ago, Goldschmidt (1940) argued that the incompatibility between micro- and macroevolution is distinct: "The decisive step in evolution, the first step towards macroevolution, the step from one species to another, requires another evolutionary method than that of sheer accumulation of micromutations". The specific solution postulated by Goldschmidt (i.e., the occurrence of systemic mutations, or macromutations yielding hopeful monsters), is excluded by current knowledge of genetics. In general, Fisher's (1930) theoretical argument, that the probability of incorporation of a mutation in a population is inversely proportional to the magnitude of the mutation's effect on the phenotype, is supported both in animals and plants. But does punctuation occur as a generally predominant phenomenon in speciation?

Punctuationists assume that mechanisms other than microevolutionary processes drive macroevolutionary processes. Punctuation theory assumes that stasis which follows the burst of the emergence of new species is due to developmental constraints and to the inability of natural selection to cause significant morphologicl changes in widespread and abundant species. The phenotypic changes during speciation are attributed to small-size population effects. Punctuationists also claim that the genetic changes during speciation are qualitatively different from those in phyletic evolution. The intertaxa phenotypic divergence is claimed to result from selection among species through differential speciation and extinction rates and to developmental constraints on the existing phenotypes (Gould and Eldredge, 1977; Stanley, 1979).

The view asserting a deep dichotomy between micro- and macroevolutionary processes has been challenged extensively since the establishment of the Darwinian theory of evolution, when Darwin (1859:432) observed that "Extinction has only separated groups: it has by no means created them". Rensch (1959:191-192) stated that one can well interpret such phenomena (i.e., morphological parallelisms) by the principles of mutation and natural selection. Charlesworth et al (1982:493) asserted that "the neo-Darwinian theory is strongly supported by the available evidence and is consistent with paleontological observations of the sudden appearance and prolonged morphological stasis of many species". Lande (1978) has shown that major morphological changes, such as the numbers of digits on limbs, can occur in a geologically rapid fashion through the accumulation of mutations. A series of Lande's theoretical papers aupport this notion (Lande, 1979, 1980, 1981, 1983). Several articles in Karlin and Nevo (1986) highlight tempo and mode processes and theory of molecular evolution.

In their critique of the paleobiological challenges to neodarwinism, Hecht and Hoffman (1986) concluded that the claims "that neodarwinism is inadequate to explain macroevolutionary patterns are unjustified. Microevolutionary processes operating within the framework of realistic boundary conditions can fully account for macroevolutionary patterns actually observed in nature. Macroevolutionary theories, which postulate reality of uniquely macroevolutionary processes (species selection, species drift, community evolution, biotic diversification at supraspecific levels, mass extinctions) are at best unfounded". Hoffman (1989) extended these arguments based on the fossil record.

Three models have developed in the framework of the Synthetic Theory of Evolution and are relevant to the concept of punctuational evolution (Grant, 1983): (i) Speciation via small isolated peripheral populations (Mayr, 1954, 1963), designated "quantum speciation" by Grant (1963); (ii) Quantum evolution (Simpson, 1944, 1953); (iii) Speciational trends, including quantum speciational trends (Grant, 1977a,b, 1989). The first of these models is given due credit by Gould and Eldredge (1977). The second is downplayed and the third is ignored completely (Grant, 1983).

Intraspecific phylogeography was advanced by Avise et al. (1987) in an attempt to bridge between population genetics and systematics, by mtDNA. The latter enables the advantage for phylogenetic analysis at the microevolutionary level. Evolutionary theory, comprising both speciation and adaptation, can bridge through mtDNA and nuclear DNA (comprising coding and noncoding regions) between micro- and macroevolution in a biologically meaningful way.

Here I will demonstrate by evidence derived from the long-term research program at the Institute of Evolution on genetic diversity in natural populations of several model organisms (primarily but not exclusively in subterranean mole rats and wild cereals) that micro- and macroevolution are not only bridged, but form an organic continuum. The problems of explaining the origin of higher categories can largely be reduced to that of explaining the emergence of a new adaptation or a set of adaptations, i.e., the shift from one adaptive zone to another (Simpson, 1953). This adaptive radiation can occur by either qualitative and/or quantitative genetic changes.

Evidence and Theory

EVOLUTIONARY THEORY AND PROCESSES OF ACTIVE SPECIATION AND ADAPTIVE RADIATION IN SUBTERRANEAN MOLE RATS, *SPALAX EHRENBERGI* SUPERSPECIES, IN ISRAEL

The inter- and multidisciplinary evolutionary model of active ecological speciation and climatic adaptive radiation of blind subterranean mole rats of the *Spalax ehrenbergi* superspecies (Spalacidae, Rodentia) in Israel has been reviewed in the light of the synthetic theory of Darwinian evolution and its current challenges (Nevo, 1991). The *S. ehrenbergi* superspecies in Israel comprises 4 chromosomal species ($2n=52$, 54, 58 and 60) displaying progressive stages of late chromosomal speciation. Their adaptive radiation in Israel from Early Pleistocene to Recent times is closely associated with the mediterranean and steppic climates, subterraneity, and an environmental gradient of increasing aridity stress, hence with distinct climatic diversity. $2n=52$ species radiated in the cool, humid northern Upper Galilee Mountains; the $2n=54$ species in the cool, semidry northeastern Golan Heights; $2n=58$ species in warm, humid central Israel; and $2n=60$ species in warm, dry southern Samaria, Judea, the Negev mountains, and coastal plains.

The ecological speciational trend of *S. ehrenbergi* into increasingly arid environments initiated apparently peripatrically in small peripheral isolates by rapid random fixation of Robertsonian chromosomal mutations. This emergence was followed by *gradual* genic accumulation of positive assortative mating based on premating ethological species-specific isolating mechanisms involving olfaction, vocalization, seismic (vibrational), aggression and mating (via bacular variation) cues. The speciational trend budded off a sequence of daughter species with increasingly higher diploid chromosome numbers (2n) towards the desert, each species displaying a syndrome of adaptations at all organizational levels. These integrated genotypic-molecular (DNA and proteins) and phenotypic-organismal (morphological, physiological and behavioural) levels as multiple adaptive strategies to the following major challenges (i) *Temporal* (seasonal annual division into dry summer and wet winter) (ii) *Local* (subterranean ecotope with its stresses of low productivity, high energetics requirements, hypoxic-hypercapnic burrow atmosphere, and total darkness), and (iii) *Regional* (gradient of increasing aridity and predictability southwards: 2n=52->58->60; and eastwards: 2n=52->54).

S. ehrenbergi represents a pluralistic example in which chromosomal genic mutations, genetic drift, migration, isolation, and natural selection all interact in producing new adaptive species in response to diverse environmental challenges. Speciation and adaptive radiation in *S. ehrenbergi* are intertwined, and are explicable only evolutionarily. We employed in our research program *proximate* reductionist approaches to construct the indispensable *ultimate* holistic organismic evolutionary model. The chromosomal species of *S. ehrenbergi* have not been named formally yet, but they represent, taxonomically, good biological species at progressively final stages of speciation. The mechanism of speciation was apparently peripatric. Post- and Premating reproductive isolating mechanisms evolved mostly allopatrically in this sequence as incidental adaptive differentiation, following the Darwin-Muller-Mayr model. Speciation involved small genomic changes, rather than a genetic revolution. It was *gradual,* not punctuational, sequentially budding daughter species in a trend along an ecological gradient. The critical adaptationist program is indispensable in understanding the evolution of *S. ehrenbergi.* Natural selection, overshadowing stochastic processes, appears to be a major architect in maintaining genotypic and phenotypic diversities and orienting *Spalax* evolution. The evolution of *S. ehrenbergi* links micro- to macroevolutuion, corroborating the Synthetic Theory of Darwinian Evolution. This is highlighted by mitochondrial DNA evolution.

Mitochondrial DNA Differentiation during Speciation and Adaptation

What is the significance of mitochondrial DNA (mtDNA) differentiation in speciation and adaptation? The magnitude of mtDNA sequence divergence varies within and between species (Avise et al.,1983). Avise and his colleagues suggested that the distribution patterns of mtDNA sequence variation within and among extant species should be of considerable relevance to the particular demographics of speciation. Is it also relevant to adaptation?

Patterns of mtDNA variation have been examined in 133 mole-rats constituting all four actively speciating chromosomal species (2n=52, 2n=54, 2n=58 and 2n=60) of the *Spalax ehrenbergi* superspecies in Israel, as well as the peripheral isolates of 2n=60 (Nevo and Beiles, 1992; Nevo et al., 1993). In the main range of the complex, a total of 28 mtDNA haplotypes were found in 64 mole-rats, with most haplotypes being unique to either a single chromosomal species or population. MtDNA divergence increased from low to high diploid chromosome number in a southward direction in Israel. Overall levels of mtDNA diversity were unexpectedly the highest in the 2n=60, the youngest species of the complex. Diversity was also greatest in 2n=60, as will be demonstrated later, for allozymes, DNA fingerprints and RAPDs (Nevo et al., 1995a). The mtDNA haplotypes can be separated into two major groups (2n=52-54 and 2n-58-60) and a phylogenetic analysis for each group revealed evidence of a few haplotypes not sorted by diploid number. The overall patterns are consistent with the parapatric or peripatric mode of speciation as suggested from previous studies of allozyme and DNA hybridization. In a separate data set, the patterns of mtDNA variation were examined across the main geographic range and across peripheral semi-isolates and isolates of the 2n=60 chromosomal species. Fifteen haplotypes were found in 69 mole-rats. High levels of mtDNA diversity characterized the main range, semi-isolated, and even some desert isolated populations. The peripheral isolates contain extensive mtDNA diversity, including novel haplotypes.

Notably, intrapopulation differences within each of the species 2n=52 and 2n=54 are of the same magnitude as the interpopulation divergence. These findings (Nevo et al., 1993) suggested that intraspecific adaptive changes in mtDNA divergence may be sometimes as big as interspecific changes accompanying speciation. Moreover, we have shown that mtDNA diversity is structured ecogeographically and biologically and is important not only in speciation but also in adaptive radiation of mole rats within and between species (Nevo and Beiles, 1992). Likewise, we have shown in Turkish mole rats that extensive karyotypic divergence occurred independently of mtDNA diversity in each of the superspecies Spalax leucodon and S. ehrenbergi. The intra- superspecies differentiation of ribosomal DNA (rDNA) was generally associated with a change in the diploid number of chromosomes, but substantial divergence in rDNA (about 1.5%) was also detected among populations of the same chromosomal species (Suzuki et al., 1995). The extraordinarily large divergence of mtDNA within each superspecies in Turkish mole rats (10% within *S. ehrenbergi* and 12% within *S. leucodon,* as against 7.4-12% between the superspecies) also suggests that mtDNA is not only involved in adaptive speciation but most importantly in adaptive radiation, in intraspecific phylogeography (Avise et al., 1987).

Genomic Adaptive Strategies within and between Species: DNA Fingerprints Reveal Ecogenetic Parallelism to Allozymes, RAPDs, Mitochondrial DNA, and Chiasma Frequency in the Actively Speciating Mole Rats in Israel

We have studied the genetic diversity structure within and between species of the *S. ehrenbergi* superspecies at the protein (Nevo and Shaw, 1972; Nevo and Cleve, 1978; Nevo et al., 1994a) and DNA levels, comprising both nuclear (Nevo and Beiles, 1988a; Nevo et al., 1995a) and extranuclear mitochondrial (Nevo et al., 1993; Nevo and Beiles, 1992) genomes.

The results of 5 genetic systems, allozymes, mtDNA, RAPDs, and DNA fingerprints of 2 minisatellite probes, involving altogether several hundreds of genes across the nuclear and mitochondrial genomes of the *S. ehrenbergi* superspecies in Israel, showed consistently the following patterns. In the Israeli species, DNA fingerprint band-diversity increased southward toward the Negev desert and eastward towards the Syrian desert. Parallel genetic patterns of increasing diversity, primarily southward and secondarily eastward, were previously shown for nuclear allozyme and extranuclear mitochondrial DNA (mtDNA) markers, RAPDs and general recombination level based on interstitial chiasma frequency. We concluded that genomic molecular evolution of nuclear and extranuclear diversities of proteins and DNA in mole rats, generally assumed to be neutral, is nonrandom and correlated positively with increasing aridity, stress, and climatic unpredictability crossing species boundaries. Gradually varying adaptive climatic selection patterns appear to be the prime driving force in both the molecular and organismal evolution of mole rats.

Most importantly, intraspecific variation of both proteins and DNA are qualitatively similar in nature and kind, and quantitatively sometimes even larger than interspecific differences. Remarkably, phenotypic divergence in morphology (e.g., general morphometrics, body size, middle ear ossicle, penile structures etc.), physiology (e.g., basic metabolic rates and respiratory adaptations), and behaviour (e.g., aggression, activity and exploratory patterns, habitat election, and mate-choice) display gradually varying patterns parallel to genotypic divergence. Often, geographic variation within a species (particularly in 2n=60 that ranges more extensively than others from semi-arid steppes to the arid deserts) is larger than interspecific differences. In other words, both qualitatively and quantitatively, *Spalax* genotypes and phenotypes do not display punctuations. By contrast, they display gradual spatial and temporal adaptive variation in accordance with increasing climatic aridity stress, both southwards towards the Negev desert and eastward, towards the Syrian and Jordanian steppes and deserts (Nevo, 1995c).

Adaptive radiation directed by natural selection to cope with climatic divergence is the key factor of *Spalax* evolution, in the twin processes of speciation and adaptation. This pattern has been demonstrated dramatically also in Turkey, whose area is 30-fold larger than Israel, and where 14-20 new *Spalax* species recently have been described (Nevo et al., 1994b, 1995b). Neither genetic revolutions nor punctuationism are needed to explain *Spalax* evolution. Natural selection to climatic stress and unpredictability in Israel and Turkey appears to be the major adaptive architect of karyotype and genetic (allozymes and DNA), as well as phenotypic (morphological, physiological and behavioural) diversity and divergence in mole rat evolution, in both speciation and adaptation. This appears to also be true for other subterranean mammals (Chaline, 1987; Nevo, 1979, 1995b), whose evolution seems primarily convergently adaptive genotypically and phenotypically, being largely unfamiliar with the critique of the adaptationist programme (Gould and Lewontin, 1979). Macroevolution appears to be a natural and gradual extension of microevolution, and not necessarily the result of differential success of certain species (and their descendants) within clades as conceived by Gould and Eldredge (1993).

Genetic Differentiation during Speciation

Genetic differentiation among the four Israeli chromosomal species of *S. ehrenbergi* was relatively very small, amounting to a "reform" rather than a "revolution." This is evidenced by very little allozyme differentiation, with very high genetic identity, *I*, of the four chromosome species (mean 0.966, range 0.931-0.988) (Nevo and Cleve, 1978), and very low genetic distance, *D* (mean 0.0197, range 0.007-0.039; see also Nevo et al., 1994a comparing Israeli and Turkish *S. ehrenbergi*). By contrast, genetic distance between Israeli and Turkish *S. ehrenbergi* was 0.104, and between *S. ehrenbergi* and *S. leucodon* was 0.234 (Nevo et al., 1994a). These estimates are corroborated by immunological distances (Nevo and Sarich, 1974) and by a DNA-DNA hybridization study analyzing the entire genome (Catzeflis et al. 1989). Likewise, *little* genomic differentiation is displayed in *S. ehrenbergi* speciation as reflected (a) in natural hybridization between the species, with differential width of the three hybrid zones; (b) in differential perfection of mate preference among the four chromosomal species; and (c) in DNA-DNA hybridization, which highlights *indirectly* the genetics of speciation (Nevo, 1985, 1991; Heth and Nevo, 1981; Beiles et al., 1984; Catzeflis et al., 1989). No information is available on the number and kind of genes which are involved in the speciation process of *Spalax*. However, the *S. ehrenbergi* complex represents a remarkable case of speciation with *relatively* few genomic changes.

The idea that speciation is associated with genetic revolution, or a major genetic genomic restructuring (Mayr, 1954), has been recognized in subsequent discussions, and particularly in recent ones, as unrealistic by Mayr himself (e.g., Mayr, 1988). It has been reviewed critically by Barton and Charlesworth (1984) and Carson and Templeton (1984), concluding that genetic revolutions are unlikely to occur during speciation. I have argued, based on allozymic (Nevo and Shaw, 1972; Nevo and Cleve, 1978; Nevo et al., 1994a, 1995a), and protein (Argamaso et al., 1995) evidence, and recently based on DNA evidence (Nevo, 1991; Nevo and Beiles, 1988a; Nevo et al., 1995a), that genetic revolution does not accompany the active speciation of various organisms, including mole rats Nevo 1989, 1991), pocket gophers (Nevo et al., 1974), or other rodents and frogs (Nevo, 1990, 1994). Similar conclusions have been drawn for other organisms by Ayala (1975) and Avise (1976). Chromosomal rearrangements (e.g., Robertsonian changes) that drive speciation in mole rats, can not be considered revolutionary changes, because they start as polymorphisms within populations (Wright, 1940) and are not associated with drastic phenotypic changes.

Linkage-group conservation appears to be the prevailing rule in vertebrate evolution (Ohno, 1984; O'Brien, 1993). Conservation of mammalian X-linkage groups in *toto*, originally proposed by Ohno et al. (1964), has now been extended to large blocks of autosomal linkage groups as well (Ohno, 1973, 1984). Chromosomal homologies comprising large blocks of autosomal linkage groups have been found between very remote species such as humans and the domestic cat (Nash and O'Brien, 1982), mouse and rat (Ringwald et al. 1994 and references therein; Hillard et al., and Beckman et al., in O'brien, 1993), and some linkage groups extend from fish to humans (Ohno, 1973, 1984). It would be of great interest to find out how much of speciation derives from the occasional breakup of previously long-conserved linkage groups and how much of speciation relates to little genic (allelic) genomic changes.

Conservation of large blocks of autosomal linkage groups from fish to mammals provide genetic evidence against the idea of genetic revolution. Speciation may indeed be accompanied by relatively few genomic changes. Even continued evolutionary divergence after the establishment of reproductive isolation, which further accumulates genetic changes, does not necessarily need dramatic changes at the DNA level. The molecular biology of *S. ehrenbergi*, involving both protein and DNA evidence, supports this conclusion. A discussion on molecular biological mechanisms of speciation appears in Rose and Doolittle (1983). Nevertheless, unravelling the genetics of active speciation, that is deciphering genes which directly cause reproductive isolation, is a future challenge. In particular, to assess the most important question of speciation genes, we need to determine if they reside in the coding or in the noncoding genome. Promising starts have been made in *Drosophila* (e.g., Orr, 1993).

Rates of Speciation

Despite their relatively geologically rapid chromosomal evolution, which certainly provided momentum to their speciation, mole rats evolved *gradually* and do not reflect the *seemingly* non-Darwinian phenomenon of punctuated equilibrium and its hallmark, stasis (see Eldredge and Gould, 1972; Gould and Eldredge, 1977, 1986, 1993); see Mayr (1988) for a balanced discussion of the theory and a moderate perspective. The evidence reviewed in Nevo (1991), based on genetics, morphology, physiology, behaviour, natural hybridization, and the rate of accumulation of ethological assortative mating is discordant with *punctuationism* and supports *gradualism.* Similar results were found for arvicolids (Chaline, 1987), other subterranean rodents (Nevo, 1995b), and mammalian species (Gingerich, 1993). The true proportion of punctuation in evolution (excluding polyploidy) remains unknown. It can hardly be assessed from the fossil record, since morphospecies do not represent biological species. Furthermore, a substantial amount of speciation is not reflected in drastic morphological changes (i.e. sibling species), and in many cases considerable morphological differentiation is not accompanied by the establishment of reproductive isolation (i.e. by speciation) (Mayr, 1988; Nevo, 1991).

Gingerich (1993) emphasized that calculation of evolutionary rates in phenotypic standard deviations per generation (haldanes) has several advantages over conventional calculation in factors of e per million years (darwins). Rates in haldanes are independent of dimension in a way that rates in darwins are not, making them more widely interpretable in terms of quantitative evolutionary genetics. Gingerich (1993) has clearly shown that evolutionary lineages in the fossil record yield intrinsic rates similar to those observed in laboratory selection experiments and natural selection in the wild. Intrinsic rates for lineages in stasis lie within the range of rates for lineages undergoing directional change. Significant long-term stasis and evolutionary change do not differ intrinsically, which means that change and stasis are determined by extrinisic environmental factors.

Many critiques of punctuated equilibrium theory have emphasized that seemingly "instantaneous speciation" events in the fossil record may have lasted many thousands of generations (e.g. Charlesworth et al., 1982; Grant, 1982; Gingerich, 1993). Neither the seemingly geological punctuations nor the apparent long periods of morphological stasis reflect all the relatively *slow population genetic* processes associated with speciation or with *postspeciational, nonmorphological* changes. These quantitatively slow population genetic changes are clearly highlighted by the ecological speciation of *S. ehrenbergi.* It involved, in the first stage, seemingly "rapid" chromosomal Robertsonian changes in small peripheral populations. However, this was followed, in the second stage, by *a gradual nonstatic* accumulation of effective post- and premating reproductive isolation, and by multiple genotypic and phenotypic adaptations to increasing aridity stresses towards the desert. Similar conclusions with respect to the gradual buildup of reproductive isolation are also drawn by Barton and Charlesworth (1984). Stasis, the most important implication of punctuated equilibrium theory (Gould and Eldredge, 1993) does not seem to be universal. Rather, it displays rates as variable as speciation itself. Moreover, as shown by Gingerich (1993) evolutionary change and stasis do not differ intrinsically and are both determined by extrinsic environmental factors.

Furthermore, while mole rat morphology appears to be *relatively* conservative, because of the underground constraints, its genetics, physiology and behaviour reflect distinct progressive differentiation related to *dynamic nonmorphological* adaptive radiation to increasing aridity stress, *far* from reflecting any evolutionary stasis, in contrast to the main emphasis of punctuationism (Gould and Eldredge, 1993). Such *nonmorphological* evolutionary dynamics are invisible in the fossil record. Mole rat speciation may have been rapid, but *neither* punctuational in origin *nor* static in evolution. It certainly fits into the framework of *gradual* ecological genetic aspects of Darwinian evolution. The latter is pluralistic in its world-view and conceives of a widespread spectrum of speciation and evolutionary rates from the gradual to the punctuational extremes [see Simpson (1944) and the critical reviews in Bengtsson (1980), Charlesworth et al. (1982); Mayr (1988), Grant (1982)], and Gingerich (1993). Even punctuations may be only *geologically* instantaneous, but *gradual* in terms of population genetics; and both stasis and change are affected by environment, representing Darwinian gradualism. However, the relative importance of different rates and/or mechanisms of speciation remain unknown for *most* species on our planet.

The Theory of Speciational Trends and *Spalax* Evolution

Evolutionary trends can take place as a result of a series of speciation events oriented in a given direction, dependent on a gradient in the environment (Grant, 1963, Chapters 18, 19; Grant, 1981, 1989). In such an environmental gradient, Grant suggested that the opportunistic speciation process tends to produce a succession of daughter species that form stages in a trend. A speciational trend has the potential for more rapid evolutionary rates than the well-recognized phyletic evolutionary trend, particularly if it proceeds peripatrically by quantum speciation. Grant (1989) asserts that the quantum speciational trend is the only macroevolutionary model known that allows for sustained rapid evolution in a given direction, and presents a few examples of such speciational trends. I wish to add to his examples that of *S. ehrenbergi.*

The ecological speciation of the *S. ehrenbergi* superspecies in Israel (Nevo, 1991) represents an excellent example of an adaptive speciational trend from ancestral species (2n=54, 52) to derived ones (2n=58, 60) along an environmental gradient of increasing aridity southward (2n=54, 52->58->60) from a mesic to a xeric environment. Each chromosomal species represents a new adaptive gene combination protected from disintegration by pre- and postmating reproductive isolation. A similar speciational trend based on chromosomal evolution was recently described in the *S. leucodon* superspecies in Turkey (Nevo et al., 1994b, 1995b). In *S. leucodon* diploid chromosome number (2n) increases from the mesic Aegean (2n=38) to semixeric Bolu (2n=54), to the xeric species (2n=62) in the central Anatolian plateau.

Directionality in *S. ehrenbergi* and in *S. leucodon* results from interspecific competitive exclusion and ecological speciation caused by the increasing aridity gradient stress, with unoccupied niches at the edge of the already occuppied gradient. The chromosomal speciation of *Spalax*, apparently in small peripherally isolated populations, led to rapid directional speciation from mesic to xeric environments by stepwise increase in diploid numbers (2n) with aridity. The higher 2n leads to an increase in the recombination index, which may be adaptive in an increasingly unpredictable ecological regime near the desert. Microevolution is transformed into macroevolution as conceived by many evolutionary biologists starting with Darwin (1859) (e.g., Mayr, 1982; Charlesworth et al., 1982, among many others).

Natural Selection and Evolution

GENERAL

Evolutionary change in organisms is affected by the interaction of several major forces, including mutation (broadly conceived), migration, natural selection and genetic drift, operating at present on past evolutionary constraints, of individuals and higher levels of organization. However, the relative importance of these evolutionary forces in the processes of adaptation and speciation of natural populations remains as enigmatic now as ever (Nevo et al., 1984; Nevo and Beiles, 1991). In 1859, Darwin suggested that the major cause of evolutionary change is natural selection. Despite the passage of 140 years, the exact nature, relative importance of diverse mechanisms of natural selection (i.e., stabilizing, diversifying, balancing etc.) in evolutionary change at single loci and multilocus structures, and its applicability to both the genotypic and phenotypic levels, are still the subject of many debates.

Gould (1982a) criticized the presumed role of natural selection in generating adaptations. He asserted that "the current utility of structure permits no assumption that selection shaped it....."Structures now indispensable for survival may have arisen for other reasons and had been "coopted" by functional shift for their new role...". "Selection may be the ultimate source of evolutionary change, but most actual events may owe more of their shape to its nonadaptive sequale". Gould's view is that "internal" factors of organic design are an equal partner with selection. This may implicate the idea that organic design was largely nonadaptive, and underestimates improvement of structures and function *over time.* Clearly, a certain amount of these past constraints must have developed by natural selection even if selective pressures were different.

For a recent critical review of the importance, abundance, and significance of natural selection in the wild, see Endler (1986, and references therein), and Williams (1992). Natural selection is also relevant for the origin of order (Kauffman, 1993). If indeed self-organization is a major evolutionary force, it must be scrutinized by natural selection, which remains ultimately the final judge of fitness and survival of the phenotype.

Studies of Natural Selection at the Institute of Evolution

Our studies in the wild during the last 20 years attempted to assess the relative evolutionary importance of selection in natural populations at both the *molecular* and *organismal* levels (Nevo, 1983, 1988a,b, 1990, 1991, 1994; Nevo et al., 1984; Nevo and Beiles, 1991). We used Israel as a genetic laboratory (Nevo, 1986) and exploited the aridity stress *southwards*, and the less severe one *eastwards* in Israel, across short geographical distances, as the ecological stressful theatre in which potential adaptive patterns can be explored. We utilized two complementary approaches in our research program. First, we examined the *regional* analysis of genetic diversity in 21 unrelated species of plants, invertebrates and vertebrates (involving 142 populations and 5474 individuals each tested, on average, for 27 enzymatic loci), sharing *similar ecologies* across a short (260 km) southward stressful aridity gradient in Israel (Nevo and Beiles, 1988b). Second, we explored the analysis of genotypic and phenotypic differentiation in four *closely related species* of the *S. ehrenbergi* superspecies in Israel (Nevo, 1991). These studies involved 4-44 populations (but usually 3 populations in each of the four species, plus one desert isolate) and thousands of individuals distributed over *different ecologies* across the same increasingly stressful aridity gradient southwards and eastwards analyzed in the first program (Nevo 1983; Nevo and Beiles, 1988b).

In our first program, we found genetic parallelism across most 21 species and most loci. Heterozygosity (both observed, *H*, and expected, *He*) was positively and, overall, significantly correlated with rainfall variation (i.e., with climatic unpredictability corroborating the niche width variation hypothesis) in both space and time. Our results were inconsistent with the neutral theory of molecular evolution (Kimura, 1983), and suggested that natural selection appears to be an important differentiating evolutionary force at the *protein and DNA molecular level.*

Likewise, in our second program, that of the *S. ehrenbergi* superspecies, overviewed here, we unravelled clinal geographic variation at all organizational levels, genotypic as well as phenotypic, suggesting the *cause* of natural selection. Climatic selection, and more specifically *aridity stress* and climatic unpredictability, appear to be the major *direct* and/or *indirect* causes of natural selection. These *maintain* and *orient* genetic polymorphisms and phenotypic diversities in natural populations. Israel can be viewed as an ecological theatre over very short distances, where the degree of aridity stress plays a major evolutionary role in genetic and phenotypic differentiation of plant and animal populations and species (Nevo, 1986). The demonstration of similar trends in some phenotypic and genotypic adaptations across xeric gradients southwards and eastwards substantiates the importance of climatic selection in *S. ehrenbergi* evolution. The paramount importance of environmental stress in driving evolution has been highlighted by Hoffman and Parsons (1991).

Even if correlations, based on a collective massive data base, are rightly interpreted as causations (see discussion in Nevo et al., 1984), they still invite complementary *critical* tests of the *specific* selection agents involved, the genetic basis of adaptations and the particular life cycles affected. The demonstration of differential viability of species that have been raised in a standardized environment, such as that for the chromosomal species of *S. ehrenbergi* (Nevo et al., 1982a), provides *direct* evidence for climatic selection. Additional biochemical and physiological studies should link physiological function to genetic molecular structure and differentiation (e.g., Koehn and Hilbish, 1987). These studies should be undertaken in an attempt to highlight the evolutionary mechanism(s) involved. Likewise, the study of polygenes that control quantitative traits (QTs) could highlight the genetic basis of adaptations (e.g. Korol et al., 1994).

Natural Selection at the Protein and DNA Levels in Local, Regional and Global Analyses

THE NEUTRAL THEORY OF MOLECULAR EVOLUTION

The neutral theory of molecular evolution (Kimura, 1983) is dualistic. At the phenotypic level, evolutionary changes are regarded by the theory as adaptive and caused by Darwinian positive natural selection. By contrast, at the genotypic-molecular level of DNA and proteins, the overwhelming majority of evolutionary changes are assumed to be neutral, or nearly neutral (Ohta and Tachida, 1990). Genetic polymorphism at the molecular level is thought to be driven by mutation pressure and random fixation (due to sampling drift) of selectively neutral or nearly neutral alleles, rather than by Darwinian selection. The theory also asserts that the majority of protein and DNA polymorphisms are selectively neutral, and that they are maintained in the species by mutational input balanced by random extinction, rather than by balancing selection (Kimura, 1983). Recently, Kimura (1989) attempted to unify the dualistic and contrasting evolutionary explanatory models of phenotypes and genotypes by a "four-stage scenario" theory of macroevolution, though he admitted that the issue is very difficult and may take many years to resolve. Unfortunately, neither his new scenario nor his previous analyses squarely face the *facts* derived from extant natural populations of plants and animals. I will briefly summarize here our own contribution to the ongoing debate on the nature of molecular polymorphisms in nature, exploiting the conclusions for the discussion of micro- and macroevolution.

Genetic Diversity in Nature: Patterns and Theory

The evolutionary significance of genetic diversity in natural populations of plants and animals was reviewed by Nevo (1978, 1988a), using the environmental-genetic correlation methodology. The reviews involve three geographic scales: (1) *Local:* "Evolution Canyon" - tests of biodiversity and genetic diversity across phylogeny (Nevo, 1995d), several species of wild cereals (Nevo et al., 1981, 1983, 1986, 1988a,b, 1994b), landsnails (Nevo et al., 1981, 1982), and barnacles (Nevo et al., 1977, 1978) in Israel. (2) *Regional:* 38 species in Israel; of these, 13 genera involving 21 species range from the mediterranean region to the Negev desert, including the 4 species of *S. ehrenbergi;* also included were two species of wild cereals in the Near East Fertile Crescent (Nevo et al., 1986; Nevo and Beiles, 1989); and (3) *Global:* 1111 species (Nevo et al., 1984) of animals and plants ranging worldwide, and 189 amphibian species (Nevo and Beiles, 1991) were reanalyzed from a literature data base. The species involved in these *local, regional* and *global* analyses are largely taxonomically unrelated. They vary in their ecologies, demographies, life histories, and other biological variables. They were mostly tested for allozymic diversity by routine horizontal starch gel electrophoresis at 25 gene loci on average (range 14-50 loci). In addition, several regional studies were reviewed on DNA polymorphisms (RAPDs, DNA fingerprints and RFLPs) in animals and plants in Israel, and the correlation was explored between RFLPs and allozymes (see the genetic systems studied at the DNA level in Table 2 in Nevo, 1991, and genetic parallelisms of nuclear and extranuclear genes, in Nevo et al., 1995a).

The following results were found at all *three* geographic scales: (i) The levels of genetic diversity vary *nonrandomly* among populations, species, and higher taxa, and (ii) Genetic diversity is partly correlated with, and predictable primarily by, *ecological* factors. (iii) Genetic polymorphisms at the micro- and macrogeographical scales, at single and multilocus structures, are similar and they are determined at all scales and levels largely by natural selection. These results corroborate the adaptive environmental theory of genetic diversity, and they were confirmed for several allozyme loci in controlled laboratory experiments on pollution biology. These experiments indicated differential viability of allozyme genotypes due to inorganic and organic pollutants (reviewed in Nevo, 1990). Furthermore, DNA polymorphisms in the nuclear and mitochondrial genomes display patterns and ecological correlates similar to protein diversity (Nevo et al., 1995a; Nevo and Beiles, 1991). Ecology can not only explain genetic indices like polymorphism and heterozygosity; it can also explain DNA sequences (Ugrinovskii, Korol and Nevo, 1995, and in preparation). The genetic patterns obtained are *inconsistent* with the neutral theory of molecular evolution (Kimura, 1983). By contrast, we have argued that natural selection in its various forms appears to be a major differentiating and orienting force of evolutionary change in protein and DNA polymorphisms. Our massive evidence and challenges were never answered by the proponents of the neutral theory.

All our field and laboratory studies during the last two decades, both in natural populations of plants and animals and in controlled laboratory pollution biology tests (Nevo, 1990) suggest that natural selection (in combination with stochastic factors and possibly other molecular forces) appears to be an important factor in maintaining and orienting molecular and organismal evolutions which are intimately linked (Nevo, 1988a,b). It is indeed astonishing how more than 140 years after natural selection was suggested by Darwin as the mechanism generating adaptations and substantiating species, so many people, including some evolutionary biologists, fail to grasp its importance in nature. They ignore the substantive considerable critical evidence, clearly and unequivocally demonstrating the key role of natural selection in evolution (see Endler, 1986; Williams, 1992). Most dramatically natural selection can override stochasticity; even in very small isolated populations (Nevo et al., 1996).

Conclusions and Prospects

CONCLUSIONS

Is a new evolutionary theory needed to explain biological evolution differently at genotypic and phenotypic levels, or at micro- and macroevolution? Are the challenges to the current Synthetic Theory of Evolution valid? Does phyletic gradualism need different evolutionary mechanisms than punctuationism? My answer to all these and other questions is that the Synthetic Theory has succeeded to explain evolutionary phenomena primarily with the ingredients of variation and selection (broadly conceived). Our studies across different groups of organisms, i.e., across phylogeny, at the genotypic and phenotypic levels at all scales, micro-, medium and macroscales, do not suggest the need for additional mechanisms. Even molecular drive (Dover, 1982) and self-organization (Kauffman, 1993) are scrutinized by natural selection, and adaptive mutagenesis (Colby and Williams, 1995, and references therein) may only enrich evolutionary theory. Speciation is only an extension of adaptation, closing genetic systems from interbreeding in variably broad ecological domains.

We and others have abundantly shown in our research program of speciation and adaptation at the genotypic and phenotypic levels that evolution proceeds through adaptive patterns. For present evolutionary biologists, as for Darwin, evolution is the conversion of the variation among individuals within an interbreeding population into variation between populations, species, and higher taxa in space and time. Background, local, regional and massive global extinctions cause gaps in the biologically continuous diversity spectra leading to higher taxa that comprise hierarchically the lower taxonomic levels. The evolutionary tree evolves from bottom to top with differential tempos and modes, depending on both phylogeny and ecology. The entire space, from very gradual to punctuational speciation, occurs in nature. Our basic ongoing ignorance relates to the relative frequency of the different slow and abrupt phenomena. Whereas polyploidy displays extreme punctuationism, most evolutionary processes, even in rapidly evolving *Spalax*, are differentially gradual. Saltationism is only an extreme of the normal evolutionary curve, as clearly suggested by Simpson (1944) for higher taxa. The same is true for speciational rates. Macroevolution ("phylogeny") is the extension of microevolution ("ecology") in space and over time.

PROSPECTS

What next? Hard and in-depth work is needed in the future on genotypes and phenotypes at micro- and macroscales at the DNA and protein levels to unravel the mysteries of genome structure and evolution. A great deal has been learned about genetic mapping from the Human Genome Project and from model organisms such as the viruses, bacteria, fungi (*Saccharomyces*), worms (*Caenorabdytis elegans*), *Drosophila*, *Mus*, and humans (see Science Genome Issues, 30 September, 1994 and 20 October 1995; and Genome Directory, Supplement to Nature 28 September 1995). At the end of this millennium and early in the next century, whole eukaryotic genomes will be sequenced, as were some prokaryotic genomes at present. Emphasis is shifting from physical mapping to large scale sequencing.

As sequences of entire pro- and eukaryotes become available, the field of comparative genomics might highlight the old problems of evolutionary biology, including the seemingly false dichotomy of micro- versus macroevolution. The polymorphisms of coding and noncoding genomic regions (presumably largely regulatory and control regions rather than junk DNA) will be opened to ecological analysis. A true integration between ecology, genetics and molecular evolution will become available. Mapping, sequencing and establishing sequence polymorphisms is a laborious task even today, when sequencing approaches 10 Mbp per day. However, only critical hard evidence together with the analysis of micro- and macroscale ecological stresses (Hoffman and Parsons, 1991) could highlight the major dichotomies and hot debates in evolutionary biology. These include the genetic basis of speciation and adaptation, micro- and macroevolutionary processes, and the patterns, modes and tempos of the evolutionary process.

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ЭВОЛЮЦИОННЫЕ ПРОЦЕССЫ И ТЕОРИИ: МИКРО- И МАКРОЭВОЛЮЦИЯ

Э. НЕВО

Ин-т эволюции, Хайфский ун-т, Мт. Кармель, Хайфа 31905, Израиль

Необходим ли новый эволюционный синтез? Дан обзор проблем темпов и генетической революции в видообразовании и соотношения между микро- и макроэволюцией. Рассматриваются примеры активного видообразования слепышей надвида *Spalax ehrenbergi* в Израиле и надвида *Spalax leucodon* в Турции. Подобным же образом на межвидовом и внутривидовом уровнях рассматриваются свидетельства генетического разнообразия в природе, основывающиеся на ранее выполненных локальных, региональных и глобальных анализах многочисленных таксонов. Делается заключение о том, что генетические революции, пунктуации (прерывистая эволюция) и стазис не являются неотъемлемыми отличительными особенностями видообразования. Видообразование может включать в себя все темпы, от постепенного (градуалистического) до прерывистого, и обычно не основывается на генетических революциях. Макроэволюционные процессы основываются на микроэволюционных процессах. Приведенные данные свидетельствуют о том, что для объяснения макроэволюционных закономерностей нет необходимости привлекать качественно новые механизмы. Синтетическая теория эволюции (СТЭ) строго поддерживается имеющимися данными на молекулярном и организменном уровнях, и только обогащается за счет них. Ожидается, что дальнейшие исследования на молекулярном уровне проложат мост между макро- и микроэволюцией и между молекулярной и организменной биологией.

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