of studied loci. The obtained values were then used in the linear regression analysis, which gave the following results:

$$H_2 = a + bk_S^{-1}, \quad b = 2.2 \pm 0.5; \quad a = -0.01 \pm 0.01$$
$$(r = 0.79; p < 0.001 \text{ with } 12 \text{ d.f.}) \qquad (10.10.6)$$

As follows from (10.10.6), the desired inverse proportionality between H_2 and k_S is indeed discovered, which means that the value of $H_2 k_S$ is conserved in all mammals, being determined by the evolutionarily conserved value of sensitivity of competitive interaction in natural populations. Note that the obtained result does not contradict the statement made in the previous section that all mammals are characterised by approximately the same heterozygosity. One may say that this statement describes the general pattern for the whole class of mammals, while results (10.10.6) reveal a more refined structure. The observed dependence (10.10.6) describes a less than twofold change in heterozygosity values between the largest and the smallest organisms. Both very large and very small mammals that are largely responsible for dependence (10.10.6) constitute a small part of the total number of mammals (see size distribution of the number of mammalian species in Figure 3.4 in Section 3.8) and cannot significantly influence the overall distribution of heterozygosity values discussed in Section 10.9.

Summing up, the performed analysis of the available empirical evidence unambiguously testifies in favour of the fact that the number of phenotypically manifested mutational substitutions (both inherited and somatic) is equally limited within large taxa of organisms with different genome and body sizes. This points to the existence of an ecological threshold of permissible level of erosion of genetic information of the natural species of the biosphere. The observed intraspecific genetic variability is a manifestation of the limited sensitivity of the process of competitive interaction of individuals, that allows slightly deleterious inherited substitutions to accumulate up to the ecological threshold.

The question of whether these substitutions may serve as the genetic basis of the evolutionary process is addressed in the following chapter.

11

Evolution

It is shown that all the available data on biological evolution are consistent with the biotic regulation concept.

11.1 EVOLUTION AND ENVIRONMENTAL CHANGE

As we have seen in the preceding chapters, all the peculiarities of organisation of living objects are aimed at conserving the existing level of order and preventing spontaneous decay of life organisation. The described mechanism of maintaining stability of biological organisation, i.e. stabilising selection based on competitive interaction of individuals in a population, may work to sustain life at a prescribed level of organisation associated with the maximum possible competitiveness without any evolutionary changes. However, if that maximum level is either not reached or does not exist, the same mechanism may bring about evolutionary changes. Random changes in genotypes, associated with loss of competitiveness, are cut off in the process of competitive interaction of individuals in the population. Random changes in genotypes, associated with higher competitiveness, provided that such take place, spread through the whole population. Progeny of more competitive individuals force individuals with unchanged competitiveness out from the population.

In other words, stabilising selection ensures propagation of the most competitive communities of species, i.e. those that are best able to stabilise their environment and are the quickest to compensate for any adverse changes in it. If the existing communities are characterised by the maximum possible competitiveness, no evolutionary changes are possible. However, the Earth's environment is exposed to the influence of various abiotic factors of cosmic and geophysical nature (e.g. changes in solar activity, rock weathering, meteorite fall, etc.), which cannot be controlled by the biota. These factors slowly change the average external conditions under which the biotic regulation of the environment takes place, making possible evolutionary changes in the biosphere.

For example, suppose that at a given level of solar activity a given ecological community is characterised by the maximum possible competitiveness, i.e. it stabilises the environment in the most efficient way. It means that no other community's organisation would ensure a quicker compensation for spontaneous environmental perturbations. When the solar activity (or any other abiotic parameter) changes, a different strategy of environmental stabilisation becomes most efficient. As a result, there opens a possibility for evolutionary changes. Evolutionary origin of new species contributes to competitiveness of the community and enhances its regulatory potential. Thus, evolution results in improved environmental regulation with respect to changing abiotic conditions uncontrollable by the biota. Note that at any time during the evolutionary process the environment remains under biotic control, be the latter ensured by either the old or a new evolutionary type of community.

The traditional interpretation of evolution is seemingly based on the same succession of events. First, the environment changes. Second, there appears a genotype which under new environmental conditions imparts increased competitiveness to its carriers and allows them to produce most progeny, forcing out other genotypes from the population. Third, this genotype gives rise to a new species (and, consequently, to a new community with altered species composition).

The principal additional statement made within the biotic regulation concept is that increased competitiveness (and, hence, increased number of progeny) is only possible when the new species that appeared in the course of evolution enhances the regulatory potential of the community. In other words, within the biotic regulation concept, competitiveness of individuals and the regulatory potential of the community to which they belong are tightly coupled (see Section 2.11). By contrast, within the traditional paradigm, an increased competitiveness (or fitness) is considered to be a sufficient condition for evolutionary changes *per se*.

Genetic information of closely related species differs by about 1% (Lewin, 1987). The average time of species existence is of the order of 10^6 years (Avise *et al.*, 1998). Consequently, during the time period of the order of 10^8 years the genetic information of the biosphere is completely renewed. This 'upgrades' the biota's ability to regulate the environment under the changing external impact of geophysical and cosmic factors. On this basis, evolution may be envisaged as another mechanism of maintenance of the regulatory potential of the natural biota, along with other stabilising characteristics of the biota that were considered in the preceding chapters.

11.2 ORIGIN OF NEW SPECIES

As shown above (Section 9.8), when environmental conditions deviate significantly from the natural conditions of the ecological niche of the species and stabilising selection ceases to operate efficiently, decay genetic polymorphism in the population may increase up to the lethal threshold. The totality of possible decay genotypes

corresponding to defective but viable individuals we called the *decay tail* of the species (Section 9.7).

We have seen (Section 10.10) that the decay polymorphism and the decay tail of the species by far exceeds the normal polymorphism. Under the assumption that the appearance of a new species' genotype is approximately the same over the whole space of viable genotypes, that means that a new species' genotype will most likely appear within the decay tail of the old species. In other words, the first individual of a new species will be with a high probability a decay individual from the point of view of the old species. Hence, such an individual will be noncompetitive under the natural conditions of the ecological niche of the old species.

Meanwhile, it is evident that an individual carrying the genotype of a new species may only survive in the population of individuals of the old species if this individual, as well as its offspring, possesses higher competitiveness compared with normal individuals of the old species. **Hence, we come to the conclusion that survival and propagation of individuals of the new species may only be ensured if the environmental conditions of the natural ecological niche of the old species are seriously distorted and stabilising selection weakened, so that both normal and decay individuals of the old species become equally competitive. In such a case, individuals of the new species (decay individuals from the point of view of the old species) will have a chance to force out all individuals of the old species, provided that the new species' individuals possess just a slight advantage in competitiveness.** This conclusion agrees with the available paleodata, according to which bursts of speciation often follow considerable environmental restructuring, i.e. transformation of the existing natural ecological niches, e.g. changing sea level, appearance of physical barriers like the Panama Isthmus, etc. (Knowlton *et al.*, 1993; Jackson, 1994).

Increase in competitiveness is associated with a higher degree of order in life processes (see Section 2.11). This factor controls spontaneous evolution of life towards its higher organisation. Possible decay changes in genotypes resulting in the decrease of order in life processes outnumber by many orders of magnitude possible changes of genotypes resulting in a higher degree of order. This statement constitutes the essence of the notion of orderliness. It is why the rate at which life orderliness decays when competitive interaction and stabilising selection are switched off should be many orders of magnitude higher than the rate of evolutionary changes.

The observed difference between the normal genomes of two closely related eukaryote species in the number of substitutions of nucleotide pairs is about 1% of the size of the genome (Lewin, 1987; Ayala and Kiger, 1984). The average difference between normal genotypes of diploid individuals of one and the same species due to limited sensitivity of stabilising selection (normal polymorphism, see Section 9.5) is also of the order of 1% of the genome size (Hofker *et al.*, 1986; White and Lalouel, 1988). Hence, the observed difference between two individuals in the number of the non-coinciding nucleotide pairs in their genomes does not contain information as to whether or not these two individuals belong to the same species. Assuming that the genome of the two kin species contains 10^9 bp, we find that the difference in the number of nucleotide pairs between both the individuals from

different species, and individuals within one and the same species, amounts to $m = 10^7$ bp. The number of different genotypes, which may be constructed on the basis of that difference, is

$$4^m \approx (10^6)^{10^6} \tag{11.2.1}$$

These genotypes correspond to normal, decay but viable and simply inviable phenotypes of individuals of both species. 'Inviable' genotypes comprise the overwhelming majority of all the possible genotypes (11.2.1), in spite of the fact that the total number of genetic substitutions does not go beyond 10^7, which corresponds to the sensitivity of competitive interaction within the population and characterises normal viable individuals in the population. The observed number of genetic substitutions tolerated by stabilising selection under natural environmental conditions is predominantly composed of slightly deleterious substitutions that have passed through the 'selection sieve' (Section 10.4). Thus, these substitutions are not random in contrast to the majority of variants of genotypes described by (11.2.1). Among the latter there are many strongly deleterious changes that are not compatible with viability of individuals.

Evidently, evolutionary transition from one species to another may only occur if the evolutionary succession of genotypic changes does not lead to loss of individual viability at any stage of the evolutionary process. One of the major questions of the evolutionary theory is whether there exists a viability 'bridge' connecting decay tails of two closely related species. In other words, the question is whether there exists a succession of separate point mutations and macromutations that could ensure transition from the initial species to a new one without loss of individual viability at any stage. If such a viability bridge does exist, gradual evolution of species is possible based on endogenic genetic modifications of the species.

If there is no such bridge between species, evolution may only occur by 'jumps' over the inviability precipice separating the two species. Such jumps mean that a certain genotype of the old species incorporates a genetic macrofragment that ensures a saltatory transition to a genotype of a viable and fertile individual belonging to the decay tail of a new species. Such a macrofragment is absent from the genome of the old species and cannot be obtained by the result of a succession of single mutational changes of the genome of the old species without loss of viability of its individuals. Such evolution by genetic 'jumps' would be manifested as punctuated equilibrium on the morphological level (Gould and Eldridge, 1993). It means that individuals of a given species retain constant morphology over the most period of the species' lifetime over geological time scale and undergo rapid morphological changes during the speciation burst corresponding to acquisition of the new macrofragment and subsequent restructuring of the genome (see below).

The new macrofragment can only be formed as a result of a multiple mutation event, when several germ-line mutations occur simultaneously in the same genome region of a newly-born individual. The probability of such a multiple event is proportional to the product of probabilities of single mutational events. Owing to this fact there exists a high probabilistic barrier that hampers evolutionary

transitions between species and, by doing so, increases the stability of organisation of the existing species. The existence of such a probabilistic barrier may explain the observed discreteness of the extant species.

Genetic information of all the extant species was once formed in the course of the evolution of genomes of species-precursors. The unique genetic information of newly-appearing species that was absent in genomes of the old species should be also written as a row of genetic letters—the four different nucleotides. The low probability of multiple mutational events imposes limits on the maximum length of a new unique macrofragment that can be obtained within a given species. Naturally, the probability to observe several mutational events within a given region of the genome is proportional to the mutation rate per nucleotide per generation and the number of individuals in the population. Accordingly, maximum macrofragments can be formed within huge populations of rapidly mutating viruses.

Let us now estimate the length of such a unique fragment formed in a population of viruses. In other words, let us discuss the following situation. Suppose that there exists a virus species which we call species A. This species can form another species, species B, if n mutations occur simultaneously in particular sites of its genome, i.e. if n particular sites of the genome of the old species are somehow changed. These n mutational substitutions represent the viability bridge between the two species. If this multiple mutational event occurs, there appears an individual belonging to species B. The question is, how long such a bridge can be, i.e. what is the value of n? If it is too long, the probability of the multiple mutational event becomes too low, and during the whole lifespan of the species A there appear no individuals with the n mutational substitutions needed to ensure the evolutionary transition to species B.

The highest mutation rate characterises RNA-viruses that cannot make use of the proofreading system of DNA repair of their hosts. RNA-viruses mutate at a rate of 10^{-4} nucleotide substitutions per site per replication (Holland *et al.*, 1982). The probability of observing n mutational substitutions in a given site of a single viral genotype is equal to $(10^{-4})^n$. Thus, to observe a genetic 'word' consisting of n new genetic letters in a given site of the viral genome we need to consider about 10^{4n} individuals of viruses. We assume the total number of viruses in the biosphere to be of the order of 10^{29}, i.e. an order of magnitude higher than that of bacteria (see Section 3.8). The average time of reproduction of viruses is of the order of 10^{-5} years. Thus, during the time period of the order of million years (the average lifespan of eukaryotic species) there appear about 10^{40} individuals of viruses. It means that the maximum length of a new genetic word prepared by viruses during this period of time is equal to $n = 10$ genetic letters ($10^{4n} = 10^{40}$). In other words, longer fragments could in principle be prepared by the use of macromutations combining unique genetic 'words' obtained by point mutations into longer 'phrases'. However, the probability of macromutations that could compose a long fragment from a non-random set of genetic words should be very low. One may therefore assert that preparation of a fragment with a prescribed succession of nucleotide pairs longer than 100 bp is absolutely improbable. Hence, all new genes (and other genome parts) appearing in the course of punctuated evolution are likely to be constructed on the

basis of incorporation of short unique fragments from 10–100 bp in length into the genome of the old species.

To investigate the question about the gradual or saltatory character of genetic evolution, let us now compare evolutionary rates in eukaryotes and prokaryotes.

11.3 EVOLUTION OF PROKARYOTES AND EUKARYOTES

According to paleodata, the average lifespan of eukaryote species is about 10^6 years (Simpson, 1944; MacFadden and Hubbert, 1988; Avise *et al.*, 1998). With the observed relative constancy of the number of species in the biosphere (Raup and Sepkoski, 1982; Wilson, 1989) extinction of every species should be compensated by the appearance of a new one which, among the eukaryotes, would differ from the old one by a change of about 1% of its genome.[1] If the genome is 10^9 bp in size, that corresponds to a change of 10^7 bp. It is natural to call these substitutions *positive*, as far as they lead to the formation of a new species and, hence, increase the level of genetic orderliness. By contrast, the overwhelming majority of possible substitutions are of decay nature and increase genetic disorder.

Estimating the number of individuals in a eukaryote species as 10^9, and assuming the time of generation to be equal to one year (e.g. a small mammal or bird), we find that there appear about 10^{15} individuals during the whole period of the species' existence. That is, about 10^8 individuals fall for every of the 10^7 positive substitutions leading to formation of a new species. Following the analogy with the rate of genome decay μ we may thus introduce the generative rate μ^+, i.e. the rate at which positive (+) substitutions are generated:

$$\mu^+ \sim 10^{-8}\,(+) \text{ substitutions per individual}$$

The rate of genome decay μ (9.1.3), i.e. the number of decay substitutions per individual (or per genome per generation, which is the same) is of the order of unity for eukaryotes (we denote μ as μ^- below):

$$\mu^- \sim 1\,(-) \text{ substitutions per individual}$$

The ratio between the decay rate μ^- and the generative rate μ^+ for eukaryotes is of the order of

$$\theta_E = \mu^-/\mu^+ \sim 10^8, \tag{11.3.1}$$

which means that during the species lifespan there appear 10^8 decay substitutions per each positive substitution out of those 10^7 leading to formation of a new species.

Now we may estimate a similar value for prokaryotes, θ_P. The average lifespan of a prokaryote species is of the same order of magnitude as that for eukaryotes, that is,

[1] Note that the nucleotide differences between any two species may be of two types. Differing sites can be dispersed over the whole genome or concentrated in some place. Knowledge about the compact type of interspecific difference is scarce because, being concentrated in some concrete places of the genome, sequences of that type are difficult to discover.

$\sim 10^6$ years (Ochman and Wilson, 1987). The size of the bacterial genome is of the order of $\sim 10^6$ bp. Kin bacterial species differ by approximately 10% of nucleotide substitutions in their genome, that is by $\sim 10^5$ bp (Ochman and Wilson, 1987). A single bacterial species contains about 10^{24} individuals (Section 3.8). During the species lifespan there appear 10^{33} bacterial individuals. Hence, there are about 10^{28} bacterial individuals per one positive nucleotide substitution, that is, the generative rate for bacteria is equal to

$$\mu^+ \sim 10^{-28}\,(+) \text{ substitutions per individual.}$$

The rate of genome decay for bacteria is of the order of

$$\mu^- \sim 10^{-3}\,(-) \text{ substituions per individual,}$$

(see Section 9.1). Hence, the ratio between decay and positive mutations for bacteria θ_P is of the order of

$$\theta_P = \mu^-/\mu^+ \sim 10^{25} \tag{11.3.2}$$

which is 17 orders of magnitude higher than the respective value for eukaryotes (11.3.1).

The difference is striking. If we envisage evolution as a continuous test of newly-appearing genotypes for their ability to give rise for a new species, we have to conclude that prokaryotes have to test almost a billion of billions of times more genotypes than eukaryotes do to form a new species.

Meanwhile, due to the universal biochemical nature of life organisation, it is natural to expect that the ratio between the numbers of decay and positive substitutions should also be a universal characteristic of life as a whole. In any case, these ratios cannot differ by those 17 orders of magnitude from eukaryotes to prokaryotes. Therefore we consider two possibilities: first that θ_E is universal, see Eq. (11.3.1), and, second, that θ_P is universal, see Eq. (11.3.2).

If we take the value of θ_E to be universal, we find that for bacteria $(\mu^+)^{-1} \sim 10^{12}$ individuals per single positive substitution.[2] Recalling that any two bacterial species differ by approximately $10^5\,(+)$ substitutions per species, we find that 10^{17} individuals need to accumulate within a single bacterial species before an evolutionary transition to another species becomes possible. Hence, during the lifetime of a bacterial individual which is of the order of $\sim 10^{-3}$ years, each bacterial species containing 10^{24} individuals would produce $10^{24}/10^{17} = 10^7$ new prokaryote species. Given that the total number of bacterial species in the biosphere is of the order of 10^4 (Chislenko, 1981), we obtain for the evolutionary rate of prokaryotes a value of about 10^{14} new species per year, or 10^7 new species per second.

Global population numbers may amount to 10^{18} individuals in unicellular eukaryotes and up to 10^{15} individuals in small invertebrates (Section 3.8). Given the average lifetime of about 10^{-2} years and the total number of lower eukaryote species of about 10^5, unicellular eukaryotes would evolve at a rate of 10^8 species per year. Small invertebrates constituting up to 10^7 species of the biosphere (Thomas,

[2] This is obtained from (11.3.1) using $\mu^- \sim 10^{-3}$ decay substitutions per individual.

1990) would evolve at a rate of about 10^7 species per year, were the value of θ_E universal. All such species would be genetically unstable and would not be capable of preserving the observed discreteness for any noticeable period of time, that is, they would not exist as biological species.

Being in drastic contrast with the available empirical data, the possibility of the universality of the value of θ_E should be rejected. We are left with the second possibility.

The universal value may thus only be that of θ_P, Eq. (11.3.2). In that case, assuming that the evolution of eukaryotes occurs exclusively by the internal (endogenic) mutational transformations of nucleotide pairs and of their macrofragments in the genome, we find that $(\mu^+)^{-1} \sim 10^{25}$ individuals per single positive substitution need to be produced on average by every eukaryote species in order to ensure an evolutionary transition to a new species.[3] However, such a great number of individuals is not produced in any eukaryote species within the lifespan of that species.

This leads one to the unambiguous conclusion that endogenic evolution of eukaryotes is impossible. Evolution (and, apparently, the origin of eukaryotes (Margulis, 1975)) may only be explained on the assumption that genomes of eukaryotes incorporate exogenic genetic material in the form of functionally sensible genetic fragments from virus and bacterial genomes (Margulis, 1975; Martin and Fridovich, 1981; Kordum, 1982; Hesin, 1984; Syvanen, 1984, 1987, 1989; Moses and Chua, 1988; Gorshkov, 1995; Amabile-Cuevas and Chicurel, 1992; Martin *et al.*, 1993; Marienfield *et al.*, 1997). Without assuming the existence of a flow of genetic information from viruses and prokaryotes to eukaryotes, there is no possibility of explaining the observed evolution of eukaryotes.

In other words, population numbers of eukaryotes are by far insufficient to ensure a gradual evolutionary transition from one species to another on the basis of a succession of endogenic mutations, even if such succession (i.e. a viability bridge between the two species, see the previous section) does exist. Thus, speciation of eukaryotes is not gradual, but occurs by a saltatory transition from one species to another. Such a transition is initiated by the acquisition of a new genetic macrofragment, which increases competitiveness of its carriers as compared with individuals of the old species. As a result, progeny of the individual that incorporated the new macrofragment exponentially forces out individuals of the old species from the population.

Note that the new, functionally-sensible macrofragment that ensures an evolutionary transition should incorporate as a single unit in an individual genotype, since separate parts of that fragment may be deprived of functional meaning and unable to impart additional competitiveness to their carriers.

Although sexual breeding may occasionally combine genetic fragments from different genotypes into a single genotype, it cannot accelerate evolution. Consider two neutral or slightly deleterious genetic 'semifragments' that produce a positive, functionally-sensible macrofragment when combined with each other. A single

[3] This is obtained from (11.3.2) using $\mu^- \sim 1$ decay substitutions per individual.

semifragment appears in the genome in the process of mutagenesis with a given probability p. The probability of the appearance of two semifragments within a single genotype is equal to p^2. It may seem that the two semifragments may unite with each other in the course of sexual breeding of their carriers with a higher probability than the probability p^2 of the double mutational event.

However, sexual partners do not know that they carry semifragments that could be combined into a single positive fragment because, as stated above, separate parts of the positive fragment do not have any effect on the competitiveness of their carriers. Thus, the two individuals carrying parts of the positive fragment may only unite by chance, the probability of that event being of the order of $1/N$, (i.e. the individual carrying the first semifragment chooses its mating partner by pure chance out of the N individuals in the population). If the population number is equal to $N = p^{-1}$, so that the probability of the appearance of a single semifragment in that population approximates unity, the probability of double event, i.e. of appearance of the second semifragment in the same genotype where the first semifragment appeared, is equal to $p = 1/N$, which is exactly the same as in the presence of sexual breeding. Thus, sexual breeding of individuals has no accelerating effect on formation of positive macrofragments that initiate speciation.

As discussed above, the average length of positive macrofragments does not exceed one hundred nucleotide pairs. Meanwhile the observed nucleotide differences between related species amount to about 1% of the total genome size, which by many orders of magnitude exceeds the length of the positive macrofragment. That means that acquisition of the positive macrofragment is equivalent to a genetic jump from the old species to the decay tail of a new species (Figure 11.1).

The first individual of the new species, the founder, is a decay individual of the new species, because its genotype differs from the normal genome of the new species in about 1% of nucleotide sites. Thus, acquisition of the positive fragment is further followed by a process of endogenic genetic changes in genotypes of the new species aimed at formation of the normal genome of the new species. This process may be called *evolutionary tuning* of the normal genome of the new species. It is practically identical to the process of genetic relaxation to the normal genome, which occurs in a population that has spent long time under distorted environmental conditions, lost some fragments of the normal genome but was then returned to its natural ecological niche (see Section 9.8 and Figure 9.3).

The only difference lies in the fact that, during the process of relaxation, the normal genome is *restored*, whereas in the course of evolutionary tuning the normal genome of the new species is *formed* for the first time, its formation being predetermined by the acquired positive macrofragment. If we represent species as potential pits (Figure 11.1), incorporation of the positive macrofragment corresponds to a jump from the initial pit corresponding to the old species onto the slope of an empty pit corresponding to a new species. The process of evolutionary tuning of the genome (i.e. acquisition of dispersed genetic differences) can be then compared with rapidly sliding down the slope of the new pit to the very bottom, where the stable normal genome of the new species resides.

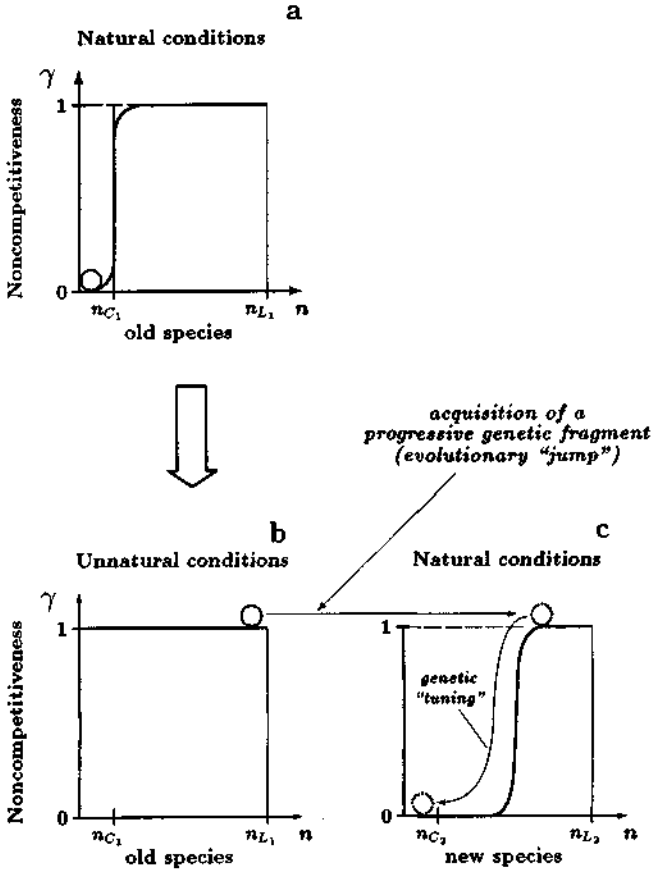

Figure 11.1. Appearance of a new species in the course of evolution. **a** – under natural conditions genotypes of the initial species randomly fluctuate around the stable normal genome of the species, $n < n_C$. **b** – under unnatural conditions normal individuals lose competitiveness, so that their competitiveness becomes equal to that of decay individuals populating the decay tail of the species, $n_C < n < n_L$. **c** – acquisition of a progressive genetic fragment by one of the individuals of the old species drives this individual to the decay tail of a new species. If the environmental conditions prove to be optimal for the new species, the normal genotype is formed in the process of genetic tuning which is analogous to the process of genetic relaxation to the normal genome (see Section 9.8 and Figure 9.3). Genetic tuning is due to increased competitiveness associated with genotypes that are most close to the normal genome. In a sexual population genetic tuning occurs very rapidly, see text.

Let us now consider the time scale of evolutionary tuning. Suppose that one individual in a population incorporates a positive macrofragment into its genome, acquires high competitiveness and becomes the founder of a new species. Its highly competitive offspring exponentially quickly force out individuals of the old species from the population. Hence, the population is soon composed of decay individuals of the new species, with genotypes including the positive macrofragment, but differing by at least 10^7 nucleotide substitutions from the normal genome of the new species.

Let us estimate the average time of tuning for a population of 10^9 individuals with genome size of the order of $G \sim 10^9$ bp and the number of divisions in the germline $k \sim 10$. Such parameters are common for many plants, invertebrates and small vertebrates. As far as the probability of a single mutation per nucleotide site per cell division is of the order of $v = 10^{-10}$, each individual in this population will carry $\mu = Gkv \sim 1$ new mutational substitution, absent from the genotypes of its parents. Thus, in a population of 10^9 individuals any mutational substitution possible in the genome (including the 10^7 positive substitutions) will be present with a high, close to unity, probability in at least one genotype. Being closer to the normal genome of the new species, individuals carrying positive substitutions become more competitive than other individuals in the population. Such highly competitive individuals tend to force out less competitive individuals from the population and breed with each other. Genetic recombination that accompanies sexual breeding results in the appearance of two positive substitutions in genomes of some of their offspring. Individuals with two positive substitutions become the most competitive, force out other individuals and breed with each other. Some of their progeny will contain four positive substitutions in their genomes and so on. As a result, normal individuals of the new species (i.e. those containing all the 10^7 positive substitutions) will dominate in the population in n generations, where $n = \log_2 10^7 \approx 23$.

Twenty-three generations of any species represent an infinitely small time period on the evolutionary time scale. Thus, we have seen that evolutionary tuning occurs nearly instantaneously, so for the majority of the time of the species' existence, its individuals retain morphological and genetical stasis (Haldane, 1954), which perfectly agrees with the punctuated equilibrium pattern of speciation observed in the paleodata (Gould and Eldridge, 1993).

The obtained result could be predicted from the biotic regulation concept. The main condition of the species' persistence and prosperity in the biosphere is its ability to stabilise the environment within the ecological community to which it belongs. Meanwhile during evolutionary tuning the species is composed of decay individuals with an impaired regulatory genetic programme. Communities with slowly evolving species with a prolonged tuning would be less efficient in environmental stabilisation and, hence, less competitive. As a result, evolution of life would be directed towards minimisation of the time of evolutionary tuning, so that any species could devote most part of its lifespan to regulation of the environment.

In smaller populations of larger organisms evolutionary tuning takes longer time. Most time is spent on the appearance of the necessary positive substitutions. In a population of 10^8 individuals, appearance of the needed substitution in a given site of the genome takes on average 10 generations, in a population of 10^7 individuals—100 generations, etc. When all the necessary positive substitutions have arisen, further tuning takes about 20 generations, as discussed above. Thus, for all species evolutionary tuning occurs nearly instantaneously compared with the average time of species existence of the order of 10^6 years, which comprises at least 10^5 generations of larger animals. Note also that all the above estimates were done under the assumption that each individual in the population produces on average one offspring, which leads to overestimation of the time of evolutionary tuning. In

reality, individuals in most species produce a large number of offspring, most of which is very short-lived (e.g. spawn in fish species). This increases the probability of the appearance of the positive substitutions in the population and shortens the time period necessary for evolutionary tuning. In endothermic animals, that are characterised by relatively low fecundity compared with other species of the biosphere, appearance of positive substitutions can be accelerated by production of a huge number of sperm cells, that may compete with each other for the possibility of egg fertilisation. Provided that spermatozoa carrying positive substitutions are more competitive, the rate of accumulation of positive substitutions in the population of mammals can be substantially enhanced.

The high competitiveness of individuals carrying single positive substitutions makes it possible for them to recognise each other and allow genetic recombination to combine all the positive substitutions in a single genotype of their offspring. Due to this fact, sexual breeding significantly accelerates evolutionary tuning. In the absence of genetic recombination, evolutionary tuning in an asexual population consisting of 10^9 individuals takes 10^7 generations (one generation per appearance of one positive substitution). Thus, asexual species deprived of genetic recombination may only appear in the course of evolution as sexual species that used to reproduce sexually but lost that ability later. Independent evolution of purely asexual species is strongly suppressed.

11.4 UNIFORMITY OF EVOLUTIONARY TEMPO IN DIFFERENT BIOLOGICAL TAXA

According to the proposed evolutionary pattern, functionally-sensible genetic macrofragments that initiate speciation in eukaryotes are prepared by rapidly-evolving viruses and bacteria. **This explains the observed uniformity of evolutionary tempo in different taxa of eukaryotes, i.e. the fact that the average lifespan of species is of the order of several million years irrespective of the population numbers, metabolic rates or body sizes of species' individuals.**

Generally, the contradiction discussed in the previous section stems from this uniformity and can be formulated in the following simple form. Why does a prokaryote species have to test almost a billion of billions of times more genotypes than a eukaryote species does, until a genotype coding for a new species is found? This striking contradiction is relaxed, when the horizontal transfer of genetic material from viruses and bacteria to eukaryotes is taken into account as the major driving force of the evolution.

This can be explained as follows. High mutability makes it possible for viruses to rapidly create positive viral fragments. Integrating into genome sequences of their hosts, viruses give them a possibility to test new positive viral fragments for compatibility with the host organism. If a new fragment appears to be positive for the host species as well, the individual with this fragment will have advantage and the fragment can be retained in the population (Marienfield *et al.*, 1997). Thus, evolution

of viruses is endogenic in the sense that viruses create their positive fragments themselves.

Higher organisms mutate and reproduce much more slowly. We have seen in Section 11.3 that if evolution of eukaryotes and prokaryotes were endogenic as well, there would be a 17 orders of magnitude's difference between the average lifespans of eukaryote and prokaryote species, which is not the case. It means that higher organisms find their positive genetic fragments much more quickly among genetic fragments delivered to their genomes by viruses than if they created these fragments themselves. In other words, concentration of positive eukaryotic and prokaryotic fragments proves to be higher in an array of positive viral fragments delivered by viruses into eukaryotic genomes than in an equally large array of all possible decay fragments generated by higher organisms themselves in the process of mutagenesis. This is not surprising. Positive viral fragments have been already tested for life compatibility in the living cell and proved to be functionally sensible, as soon as they were able to ensure formation of a new virus species. Meanwhile endogenic genetic fragments formed during mutagenesis in genomes of higher organisms represent decay of genetic information and loss of function of previously meaningful genetic fragments.

Hence, the limiting factor of evolution in both prokaryotes and eukaryotes is the creation of functionally sensible genetic fragments by viruses. As soon as the limiting factor is the same, the evolutionary tempo is the same as well.

The proposed evolutionary pattern explains the observed relatively constant rate of genetic substitutions in homologous genes of different eukaryote as well as prokaryote species, i.e. the so-called 'molecular clock' (Zuckerkandl and Pauling, 1965; Kimura, 1987; Ohta, 1987; Zuckerkandl, 1987; Ochman and Wilson, 1987; Ayala, 1999). In many cases, the time various contemporary species have taken to diverge from a common ancestor is known from paleodata. The observed differences in the nucleotide sequences of homologous genes of the two species, divided by the time of their independent evolution, gives the doubled rate of molecular evolution of each species, i.e. the absolute rate of appearance of positive substitutions in the species' genomes. Comparing several pairs of such species with different times of divergence, one may find the average rate of molecular evolution during various time periods. These rates appear to be roughly the same for different evolutionary lineages, and that effect is essentially what the 'molecular clock' is about.

Within the proposed evolutionary pattern, such an effect is simply due to the fact that the average relative genetic distance between closely-related species appears to be approximately the same in different taxa; meanwhile the average lifespan is approximately the same for all species being determined by the rate of appearance of new positive genetic fragments in viral genomes. Dividing approximately equal values of evolutionary genetic distance (i.e. the number of positive genetic substitutions) by approximately equal values of the species' lifespan, we naturally arrive at approximately equal values of the absolute rate of appearance of positive substitutions per year. Note, however, that taking into account the saltatory character of the evolutionary process, the absolute rate of appearance of positive substitutions appears to be a non-informative characteristic when averaged over the whole time

of species existence. The overwhelming majority of positive substitutions appear in the course of evolutionary tuning (Figure 11.1) shortly after acquisition of a positive macrofragment that initiates speciation, while during the remaining time of the species' existence no directional changes take place in the genome. Thus it makes no sense to speak about the average number of substitutions per year during the whole lifespan of a species.

11.5 CONCLUSIONS

Taking into account the fact that for the majority of the time of their existence all species remain in a state of evolutionary stasis, the problem of tempo and mode of evolution is of but secondary importance to the biotic regulation concept. The biotic regulation concept pertains mostly to the everyday existence of species and their everyday work on stabilisation of the environment.

However, we considered it necessary to briefly discuss in this chapter the major empirical data on evolution. This was done in order to show that all of them find an explanation within the biotic regulation concept. In other words, the existence of evolution neither discredits the biotic regulation concept nor provides evidence for genetic adaptation of species to the changing environment. Moreover, the proposed evolutionary pattern that arises from the central genetic issue of the biotic regulation concept, namely that of genetic stability of species which is necessary for stabilisation of an optimal environment, provides explanation for some evolutionary questions (like that of uniform evolutionary rate in prokaryotes and eukaryotes) that still remain even unaddressed within the traditional biological paradigm.

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Conclusions: Can the Biosphere Be Treated as a Resource?

Humans are unique in the living world. Unlike all other species, humans are able to accumulate cultural heritage, which is transmitted to following generations. Accumulation of cultural heritage is not only a unique ability of *Homo sapiens* individuals, but one of their natural needs encoded into the species genome. The development of cultural heritage cannot be stopped. Were the cultural information cease to accumulate, that would mean termination of the existence of the *Homo sapiens* species.

An inherent component of the development of cultural heritage is scientific and technological progress. Its modern rate can be characterised by the average time of replacement of major technologies, which is now of the order of several years. The corresponding natural process of replacement of biotic 'technologies' (i.e. the ways of the biota's organisation and functioning) is characterised by the average evolutionary time of complete change of the genetic programmes of the extant species, which is of the order several hundred million years (Chapter 11). Thus, the contemporary rate of scientific and technological progress exceeds the rate of evolutionary progress by 7–8 orders of magnitude. Any possibility of sustainable development of the biosphere in pace with the development of humanity is therefore unthinkable. The misleading idea of such a possibility is based on erroneous identification of relatively rapid processes of decay and relaxation of the genetic information of natural biota (including artificial selection of domestic plants and animals) with natural evolutionary processes (Chapters 9, 10 and 11).

Thus, humanity is facing two contradicting phenomena—the inevitability of development of civilisation and the impossibility of an equally rapid development of the biosphere. In other words, while civilisation develops, the biosphere degrades. To solve the contradiction, one needs to confine civilisation's development within such limits that would make it possible to ensure the safe existence of the biosphere, i.e. the biota and its environment. In order to do it, one needs to quantify the permissible threshold of anthropogenic perturbation of the biosphere beyond which the biotic regulation of the environment ceases to operate on a global scale and global environmental changes commence. This threshold, in the first approximation,