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Diversity and Development: Tempo and Mode of Evolutionary Processes

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ABSTRACT

A simple model of evolutionary processes (i.e., processes showing far-reaching analogies with biological evolution) and the results of a simulation study of the model are presented. The model consists only of the main features of evolutionary processes and has been worked out for a special purpose: to show how the tempo and mode of evolutionary processes depend on the population diversity in which those processes take place. The long-range mode of development of evolutionary processes is a rough one, characterized by two successive phases: a quasi-equilibrium phase and a substitution phase. In the quasi-equilibrium phase, two parallel processes act: very noticably, a process of gradual improvement of existing types, and in the background, a searching process of new basic improvement. In the substitution phase the new basic improvement supersedes the old type and the system goes to a new quasi-equilibrium phase. Compared to the length of the quasi-equilibrium phase, the duration of the substitution phase is very much shorter and looks like a leap. Duration of the quasi-equilibrium phase is greatly influenced by chance and its probability distribution depends mainly on the population diversity.

The two opposing mechanisms—selection and generation of types—determine the population distribution within the parameter domain. The distribution consists of the center (the "best" type elements) and the neighborhood. The main source of improvements (innovations) lies in the neighborhood; that is, the "worst" elements.

The two main strategies of development—short-sighted and far-sighted—have been identified.

Introduction

The existence of far-reaching analogies between biological evolution and processes of human activity, such as science and technological development and evolution of natural languages, is commonly accepted [3, 8, 13, 15, 16, 20]. These analogies are noticed at many levels—individual, population, species, and the development of whole systems—and, what is most interesting, all these analogies are observable in spite of basic differences in causative mechanisms of these processes. General theories of evolution have been worked out. As an example, the work of Csanyi [4] may be cited, in which molecular evolution, evolution of ecosystems, and cultural and technical evolution are considered; at the end the general theory of evolution and basic laws of evolutionary processes are presented.

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Waddington [23] considers one of the most important properties of living and artificial systems. He writes:

> A natural living system has usually acquired some degree of stability by natural selection (it would have fallen apart and died out if it wasn't stable enough); in artificial systems man commonly designs a series of checks and counter-checks to ensure stability. An important point to note, however, is that the stability may not be concerned with preserving the measure of some component of the system at a constant value, as in homeostatic systems. The stabilisation of the progressive system acts to ensure that the system goes on changing in the same sort of way that it has been changing in the past. Whereas the processes of keeping something at a stable, or stationary, value is called homeostasis, ensuring the continuation of a given type of change is called *homeorhesis*, a word meaning preservation of a flow.
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> A phrase used to describe such systems, is to say that the pathway of change is canalised. For the pathway itself one can use the name *chreod*, a word derived from Greek, which means "necessary path." . . . Different canalised pathways of change may have rather different types of stability built into them. These can be pictured in terms of the cross-section of the valley. You may, for instance, have a valley with a very narrow chasm running along the bottom, while the farther up the hillside you go, the less steep the slope. With such a configuration of the attractor surface, it needs a very strong push of some kind to divert a stream away from the bottom of the chasm. . . . In contrast, we have a valley which has a very flat bottom, and the hillside gets steeper and steeper as you go away from the central stream. Then, minor disturbances can easily shift the stream from one side of the flat valley to the other; it would be rather a matter of chance where in the water-meadows in the valley bottom it flows.

The model of evolutionary processes presented in this paper does not pretend to be a general approach to these process types. The model consists only of the main features of evolutionary processes and has been worked out for a special purpose: to show the ways in which the tempo and mode of evolutionary processes depend on the population diversity in which these processes take place.

In our understanding, the main features of evolutionary processes are as follows:

1. They take place in a relatively large set of congeneric elements (individuals) acting in some limited-capacity environment and fulfilling the same task (performing the same role); examples are elements of biological species and products of some technologies supplying the same human need (technological species[1]);
2. Elements have finite lifetimes (as in biological systems); after this time, elements are withdrawn from the environment and are replaced by new ones during the reproduction process;
3. Each element is a unique unit, but one can divide the population into separate classes containing almost identical elements (genotype in biology or products of the same technology). We will say that the elements of the same class are of the same type;
4. Elements are valued differently by the environments in which they act. The preference depends on a quality of the task fulfillment (fitness is the measure of preference in biology). Generally, preference is a random variable, different for different elements, but one may expect that the average evaluation is equal for

[1]We would like to propose the following interpretation of the meaning of technological species. The definition of basic innovation given by Mensch [14] states that "technological basis innovation creates new markets and new industrial branches." In this context, emergence of a basic innovation is analogous to emergence of a new species, a technological species. Another common property of technological and biological species is the clustering of their occurrence; see, for example, Mensch [14], in which the statistics of basic innovations are presented, and Bombach [2], in which the temporal occurrence of biological species is shown.

all the elements of the same type. Therefore, we may talk about better and worse elements;
5. During the reproduction process the statistical possibility of changing the offspring type (a modification) exists; this leads to the possibility of emergence of a new type (new genotype or new technology).

The last two points show two opposing mechanisms: selection of types and generation of types. Generally, these two processes are random ones comparable to the trial-and-error process.

Evolution and revolution are two modes of development that are by common understanding totally opposite. Is this valid? Aren't they two aspects of the same phenomenon? Isn't the phenomenon governed by the same mechanisms?

The concept of evolutionary mode development prevailing in Western thinking [7] postulates the existence of continuous, even changes, consistent with the Linneaus statement, *natura non facit saltum* (nature does not make leaps).

But a more detailed observation of nature yields a new picture of the world; features that are claimed to be in a continuous state are discrete. From the beginning of the twentieth century, the new quantum theories gained approval. Theories of non-continuous time and space have appeared. One may say that this is relevant to the microworld, but the same tendency of expanding non-continuous thinking is noticeable at the macro scale. Probably the best known theory of social development, in which the existence of leaps (revolutions) is postulated, is the theory by Marx and Engels. It is especially visible in their second principle of development, borrowed from Hegel, which states that the new quality emerges by leaps as the result of a slow accumulation of quantitative changes; that is, the law of transformation of quantitative changes into qualitative ones.

Attempts have been made to build mathematical theories of non-continuous development; the best known is Thom's catastrophe theory [21]. Many examples of the application of this theory to a description, or explanation, of the development of many systems may be given. For our purposes it is enough to mention the biological applications of Dodson [5] and Waddington [22] and the economic application of Mensch [14] to the description of economic crises.

Similarly, systems theory, with its concepts of steady state, equilibrium state, homeostasis, and feedback, among others, postulates, in a non-explicit way, the existence of rapid transition during systems development.

We must emphasize that we do not claim that all changes are non-continuous; we would only say, with Gould and Eldredge [7], that the most essential changes in long-range development are not the long phases of gradual changes but comparatively short phases of very rapid development (leaps), conducting systems to qualitatively new equilibriums.

In our understanding, the development of any evolutionary system is cyclical, with two phases in every cycle: the quasi-equilibrium phase and the substitution phase. At the quasi-equilibrium phase, some gradual changes are visible, but these changes are much less important than the coming (expected) ones. In this phase, the searching process of new basic improvement is the most important, however not clearly visible; that is, improvement the occurrence of which radically changes the whole system structure (in our terminology, the emergence of a basic improvement is equiponderate to new, better type emergence). At every stage of evolutionary systems development, the actual types are bases for the search of new, better types. As we mentioned earlier, this searching process may be compared to the trial-and-error process. As a rule, we may say that the parameters characterizing the best existing type are so tuned that changes in a small number of parameters in this type do not lead to improvement. New and better solutions require simultaneous change of quite a large number of parameters. The probability of simultaneous changing of so many parameters is relatively small (the relationship between the probability of changing of some set of parameters and the number of these parameters is a geometrical one). The emergence of a basic improvement causes a rapid change (leap) in any relevant, global measure of the system's development. The leap occurs at the substitution phase; during this phase, a new, better type supersedes the old one, and the system goes to a new quasi-equilibrium. The duration of the substitution phase is much shorter than the duration of the quasi-equilibrium phase.

A new, basic improvement contains only the main idea of its future development; we may say that the first feature of a basic improvement is strange, dwarfed, and non-proportional (using the anthropological point of view). The first form is the base of its future improvements, proceeding parallel to the searching process. As we said, in this period (i.e., at the quasi-equilibrium phase) gradual development connected with the incorporation of small improvements of the base form is the most noticeable. The probability of occurrence of these improvements is comparatively great (mainly because not so many parameters need changing to find a better solution) and occur quite frequently. The influence of these improvements on the system's development, however, reflected, for example, in a constructed global measure of system development, is much smaller than the basic improvement's influence.[2]

This article is based on the results of works carried out from 1975–1979 [see 6, 10, 11]. Quite recently, we found that very similar ideas on mode development of evolutionary processes are represented, in biology by Gould and Eldredge [7] in their theory of punctuated equilibria and in technology by Sahal [19], Reece [17], Leithwaite [12], and Bell [1]. For example, Sahal writes,

> As regards the process of technological change, very often there emerges a pattern of machine design as an outcome of prolonged development effort. The pattern in turn continues to influence the character of subsequent technological advantages long after its conception. Thus innovations generally depend on bit-by-bit modification of a design that remains unchanged in its essential aspects over an extended period of time. The basic design is in the nature of a guidepost charting the course of innovative activity.
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> The notation of a technological guidepost is evidenced by the fact that very often one or two early models of a technique stand above all others in the history of an industry. Their design becomes the foundation of a great many innovations via the process of gradual evolution. In consequence, they leave a distinct mark on a whole series of advances in technology. [19, p. 33].

In the following sections we present the description of a simple mathematical model of evolutionary processes, some examples of its simulation (more results may be found in [10, 11], and an approach to evaluation of the tempo of evolution. Finally, the general conclusion and proposals for future research are presented.

[2]Each improvement gives as an effect a leap of the development of a system, but frequently the effects of each improvement are small and overlap one another, so that the overall effect seems to be continuous (gradual). The following row hypothesis may be constructed: every evolutionary system, independent of its evolution phase, develops by leaps; commonly, leaps are so small that they are undetected or vanish in statistical noise. With many almost simultaneous improvements, their effects overlap—so the overall development seems to be gradual. The relationship between the importance of the innovation (leap) and the probability of its occurrence is inversely proportional: the "greater" the leap the less its probability of occurrence.

I. Model

We consider development of a population of congeneric elements, acting in a well-defined environment.[3] We assume the existence time of each element (a finite lifetime). After this time the elements are reproduced; in the reproduction process the "old" elements (i.e., the previous generation of elements) are replaced by the new generation (the offspring). The number of offspring of every element is a random variable with given distribution. Therefore, it may be said that we assume nonoverlapping generations and discrete time. The population is divided into separable subsets, which we call types. All elements fulfill the same task in the environment, but the quality of this task fulfillment is different for different elements. Generally, the quality index is a random variable, but to simplify the calculation process we assume deterministic, time-invariant indices and the same value of the index for all the same type elements.[4]

We assume that every element is characterized by an n-dimensional vector of parameters $d = (d_1, d_2, d_3, \ldots, d_n)$; each coordinate d_i, $i = 1, 2, \ldots, n$, belongs to an infinite set of discrete values. Without loss of generality, we assume for simplicity integer values for the scope of all parameters. The inclusion of the parameter domain $D^n = (d = (d_1, d_2, \ldots, d_n), \forall_i\, d_i \in C)$ enables the division of the population into postulated separate subsets (types). All elements characterized by the vector of the same parameters are the same type elements. We postulate an existence of a quality function q differentializing the quality of task fulfillment by all types defined by the parameters' domain. The quality function has positive real values with zero (i.e., $q : D^n \rightarrow R \cup (0)$) and describes the environment's relative preferences, visible during the reproduction process: statistically, the greater the quality index, the more offspring of the element.

For each two elements of type d, the distributions of offspring number are the same and are statistically independent. The expected value of offspring of the elements of type d is proportional to the quality index of type d, $q(d)$.

Not all offspring of the d-type element have the same type d; during the reproduction process the statistical possibility of a type changing exists (type modification). The probability of type modification from type d to d', $p_{dd'}$, is relatively small and quickly diminishes as the d–d' distance grows. A geometric relationship between the modification probability and the distance may be expected.

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[3]From the biological viewpoint the model presented describes the evolution of a haploid population living in a stable environment in which no recombination process works. Recombinations accelerate the tempo of evolution significantly and in future model development they should be included. In our opinion, however, a recombination process does not change the final conclusions of this article, especially concerning the mode of evolution and the importance of the diversity in the development process.

An almost general feeling of much higher tempo of development of artificial (human) systems exists in comparison with the tempo of biological evolution. This is only a feeling and needs further deep investigation. If true, it seems that three main factors have the most significant influence on the speed-up: (1) "the memory" of past experiments and past development in biological systems reaches only one generation, contrary to many generations of memory in human systems; (2) in biological systems, the recombination process is limited to recombination within the species (i.e., very similar individuals), and in human systems this is not valid. Many examples of recombinations exist within quite distant elements (synergetic effects); and (3) "communication" (understood as the possibility of two individuals meeting to give "offspring") is much more limited in biological systems (e.g., geographically). The importance of this factor is visible in the acceleration of technological development during the last 200 years, connected, among others, with the growing possibilities of communication.

[4]It has been shown [9] that an essential influence on long-range development is the average value of the quality index level. Assuming different conditions of change of the quality indices (e.g., random, periodical, trend changing) providing the same average value, the differences of population development were negligible.

A limitation exists on the population-growth ratio: we assume that the expected number of elements after the reproduction process is proportional to the number of elements before reproduction: that is,

$$E\,[N_\Sigma\,(t+1) \mid N_\Sigma(t)] = g * N_\Sigma(t), \tag{1}$$

where:

$N_\Sigma(t)$ = total population at time t, and

g = proportional ratio (the dependence of the ratio on the capacity of the environment, the maximum reproduction ratio, and other factors may be assumed).

On the base of the above assumptions, a conditional distribution of the number of all types (i.e., the distribution of the state of population) at time t may be calculated. Detailed descriptions of the distribution's calculation is presented in Kwasnicki [11]. For our purpose, it is sufficient to say that the conditional probability-generating function (p.g.f.) of the population state is

$$G\,(s\,,\,t+1) = \prod_{d \in D^n} \left[f_d \left(\sum_{d' \in D^n} p_{dd'}\, s_{d'} \right) \right]^{N(d,\,t)}, \tag{2}$$

where:

s = n-dimensional complex number matrix, corresponding to D domain; for each type d the related complex numbers exist;

$f_d(.)$ = p.g.f. of offspring of d-type element;

$N(d,t)$ = number of d-type elements at time t; and

$p_{dd'}$ = probability of modification of the type.

On the basis of p.g.f. $G(s\,,\,t+1)$, the expected value of d-type elements at time $t+1$ may be reckoned:

$$E[N(d\,,\,t+1)] = \sum_{d \in D^n} g * N(d'\,,\,t) * [q(d')\,/\,Q(\mathrm{t})] * p_{dd'}, \tag{3}$$

where:

g = the proportional ratio in Equation 1;

$q(\mathrm{d})$ = the quality index of type d; and

$Q(\mathrm{t})$ = the average quality index at time t.

$$Q(t) = \sum_{d \in D^n} [N(d\ ,\ t) / N_{\Sigma}(t)] * q(d). \qquad (4)$$

The model presented above describes the optimizing process in the D^n domain. In the course of time, the number of elements with quality indices greater than the actual average quality grows; simultaneously, the elements with indices lower than the average quality are superceded. The mechanism of type modification provides the possibility of emergence of new and better as well as worse types, and in the stable environment (i.e., in our notation in the case of time-invariant quality function) the average quality is a non-decreasing function of time.

In our opinion the expected value of the population state (Equation 3) offers no information about the most significant and the most interesting feature of the evolutionary processes, especially concerning the tempo and mode of the processes. The most significant features are observable in the process realization, therefore, we choose the simulational technique to investigate these processes.

II. Simulation

All simulational experiments presented in this section have been carried out under the following assumptions:

1. Constancy of the expected population number; therefore the population ratio g in Equation 1 is equal to 1;
2. A Poisson distribution of the offspring number; therefore, the p.g.f. of the offspring number in Equation 2 is equal to

$$f_d(s_d) = \text{EXP}\{[q(d) / Q(t)] * (1 - s_d)\};$$

3. Probabilities of type modifications

$$p_{dd'} = \begin{cases} 0 & \text{for} \quad \| d - d' \| > n \\ p^{\| d - d' \|} & \text{for} \quad 0 < \| d - d' \| < n \\ 1 - \sum p_{dd'} & \text{for} \quad \| d - d' \| = 0 \\ d' \in D^n \text{ and } d' \neq d & \end{cases}$$

where the distance between d and d' is defined by

$$\| d - d' \| = \sum_{i=1}^{n} \text{ABS}(d_i - d'_i);$$

4. The shape of the quality function is essential for the process development mode, and a relevant way of its selection is very important for correct interpretations of the results. Choosing functions with a shape similar to a long, sharp ridge, not parallel to the axis of the D^n domain seems the most relevant; frequently, a process development is described in terms of changing the values of the chosen parameters. The parameter values are so tuned that to find a better solution (improvement), the simultaneous change of a relatively large number of parameters is required; change of an insufficient number of parameters leads to wors-

ening of quality. The postulated shape is also consistent with the shape of Waddington's chreod [23], reflecting the fitness function (epigenetic landscape); and
5. At the initial moment the population consists of only one type individual.

II.1. TYPICAL FEATURES OF EVOLUTIONARY PROCESSES

Development of evolutionary processes is the result of simultaneous actions of two opposing mechanisms: type selection and type generation. The first mechanism causes the growth of better types (in our model, types with qualities greater than the average quality and the growth rate increases with the ratio $q(\mathrm{d}) / Q(\mathrm{t})$). Simultaneously, the worse types are superseded. The selection mechanism causes the reduction of population diversity, and so the tendency to a single type within the population (i.e., the best one). The second process issuing from the possibility of type modification during the reproduction process causes the emergence of new, better, and worse types and the increase of population diversity (as the consequence of this, the average quality diminishes).

Stabilization of some population distribution within the parameter domain D^n, with the center consisting of the best types of elements and the neighborhood consisting of the worse types, is the result of concurrence of these two mechanisms. The local shape of the quality function and the probabilities of type modifications mainly influence the population distribution in D^n (the influence is especially visible in the value of the dispersion of the distribution). The local shape of the quality function (gradient) reflects the tolerance of environment; the lesser the gradient, the more tolerant the environment. Greater tolerance causes greater population dispersion. Similarly, the greater the modification probability, the greater the dispersion.

The existence of dispersion diminishes the average quality and, from the viewpoint of temporary population development, is disadvantageous. On the other hand, as simulational experiments reveal, the population dispersion has a very strong influence on the probability of emergence of better types. The greater the dispersion, the more frequent the emergence of new, better types. Thus, process development is a compromise between temporary diminution of average quality and a preparation of a base for faster development of the system in the long range.

The experiments carried out under the following conditions illustrate typical features of the simulated process:

1. Two-dimensional quality function ($n = 2$)

$$Q_1(d_1 , d_2) = \mathrm{EXP}\{-0.01 \bullet [(d_1 + d_2)^2 + (d_1 - d_2)^2]\} \tag{5}$$

A map of this function if shown in Figure 1.

2. Probability of modification $p = 1.5 \bullet 10^{-3}$,
3. The initial population consists of type (15 , 15); $N[(15 , 15), 0] = 10^4$.

Two exemplary population distributions in D^n domain are presented in Figure 2. The distribution at $t = 110$ is an example of a typical distribution at the substitution phase. The center of population and the neighborhood shifts from point (8 , 8) to point (7 , 7). The second distribution at $t = 250$ is an example of a distribution at the quasi-equilibrium phase. The center is in (4 , 4). A new, better type (3 , 3) has not yet been found; the neighborhood consists of six types: (3 , 4), (4 , 2), (4, 3), (4 , 4), (4 , 5), and (5 , 4). On the axis the distributions of parameters d_1 and d_2 for these two generations

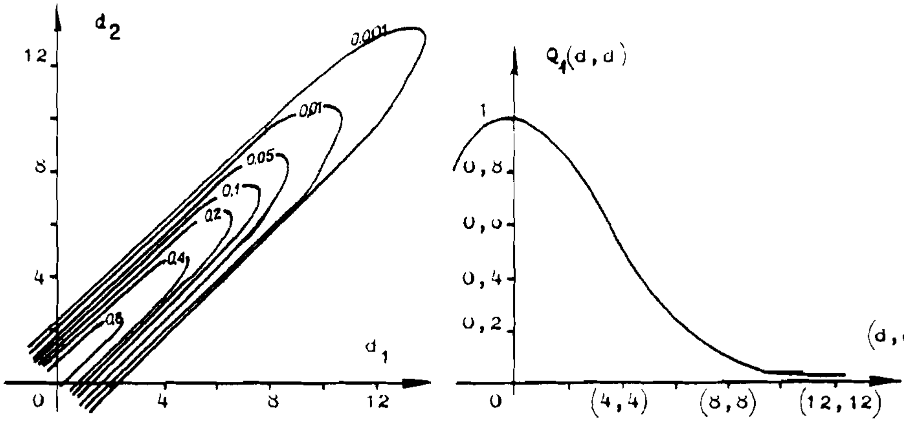

Fig. 1. Map and profile along the ridge of the quality function Q_1.

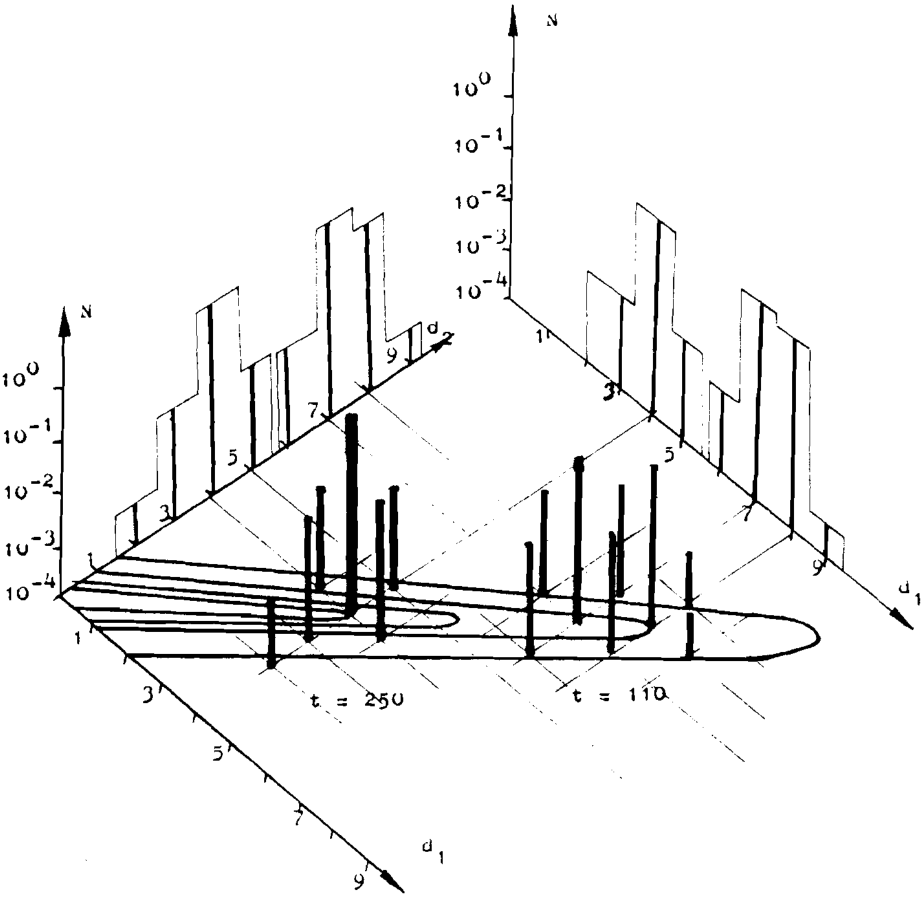

Fig. 2. Exemplary population distributions of substitution phase and quasi-equilibrium phase.

are indicated (note the logarithmic scale of the number of elements). The expected values of the parameter distributions mark the population trajectory in the D^n domain. Typically, the trajectory moves along a ridge of the quality function; in the case of a distant population the quick development of population toward a ridge is visible; after reaching a ridge the population develops along the ridge with relatively less tempo. It may be said that a ridge is the strong attractor of the development of the population.

The shape of the quality function q has been so chosen that changes of either d_1 or d_2 parameters for types on the ridge diminish the quality index; to find a better type, a simultaneous change of two parameters is required. The modification probability is equal to $p = 1.5 * 10^{-3}$, and in the case of one type population (i.e., consists of a type on the ridge) it may be expected that a new, better type occurs every 45 generations.

But another way of finding a better type exists, requiring only one parameter modification in relevant types within the neighborhood. In the phase of quasi-equilibrium at these two points there exist 150 elements. The quality of these types is equal to 0.8 of the quality of the best one; in every generation 30 elements are superseded and 30 elements are introduced as the effect of the best type modification. We may expect that those 150 elements bring a better solution every four generations.

The main source of improvements, therefore, is clearly the neighborhood of the best, dominating type, not the best type itself. The profit is much higher for larger dimensions of the parameter domain; this will be shown in further experiments and also in the next section, in which an attempt is presented to evaluate the tempo.

The "history" of type development is shown in Figure 3. The gain and loss of domination of types (7 , 7), (6 , 6), (5 , 5), and (4 , 4) is evident at all times in the background of the dominating types. Noise exists, consisting of the worse types (i.e., the surrounding). Their number is a small fraction of the total population, but we may say that the noise has a vital importance for the future development of the system. The average quality is shown in Figure 4; moments of the emergence of new, better types are indicated by arrows. The dispersion of one parameter is also traced in the figure. The correlation of the phases of rapid growth of the average quality with the emergence of

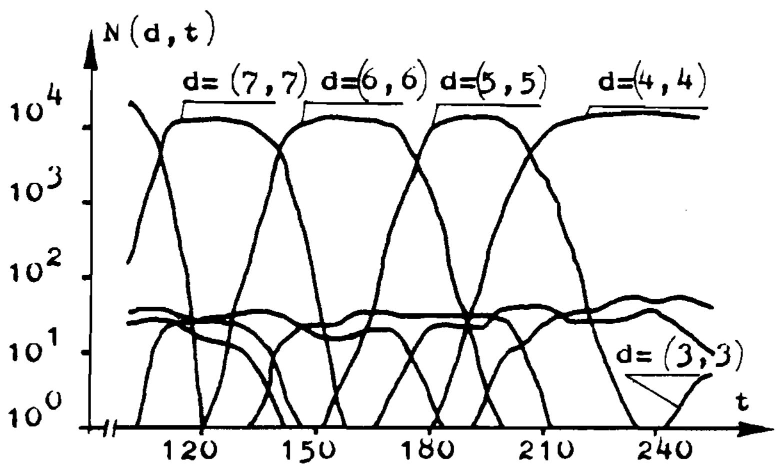

Fig. 3. Temporal type development.

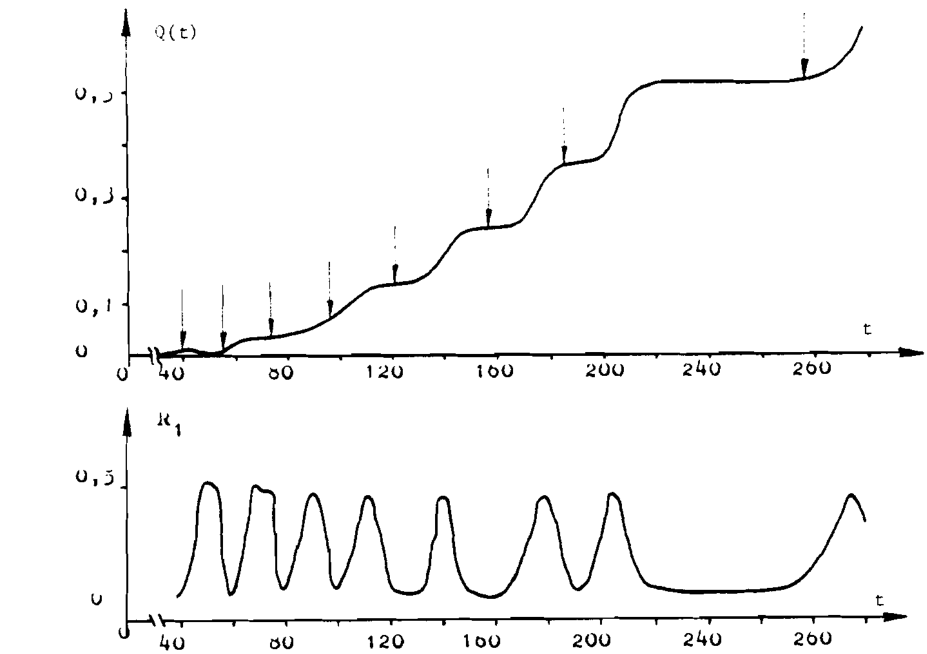

Fig. 4. Average quality and d_1 parameter's dispersion in experiments with quality function Q_1.

better types (the beginning of the substitution phase) is noticeable. The lowest level of dispersion is observed in the quasi-equilibrium phase.

II.2. TEMPO AND MODE OF POPULATION DEVELOPMENT AND THE DIMENSION OF THE PARAMETER DOMAIN

Some experiments with two, three, and four dimensional domains have been conducted.[5] The quality functions for these experiments are:

$$Q_2(d_1, d_2) = \mathrm{EXP}\{-0.1 * [\mathrm{ABS}(d_1 + d_2) + 2 * \mathrm{ABS}(d_1 - d_2)]\}. \tag{6}$$

$$Q_3(d_1, d_2, d_3) = \mathrm{EXP}\langle -0.067 * \{\mathrm{ABS}(d_1 + d_2 + d_3) + 2.5 * [\mathrm{ABS}(d_1 - 0.5 * (d_2 + d_3)] + \mathrm{ABS}[d_2 - 0.5 * (d_1 + d_3)] + \mathrm{ABS}[d_3 - 0.5 * (d_1 + d_2)]]\}\rangle. \tag{7}$$

$$Q(d_1, d_2, d_3, d_4) = \mathrm{EXP}\langle -0.05 * \{\mathrm{ABS}(d_1 + d_2 + d_3 + d_4) + 1.5 * [\mathrm{ABS}(d_1 + d_2 - d_3 - d_4) + \mathrm{ABS}(d_1 - d_2 + d_3 - d_4) + \mathrm{ABS}(-d_1 + d_2 + d_3 - d_4)]\}\rangle. \tag{8}$$

[5]Direct simulation (i.e., simulation in which all possible types are considered) consumes a great amount of computer time and computer memory for a larger-than-four-dimensional parameter domain D. In direct simulation methods for a larger dimension domain are in the process of being developed.

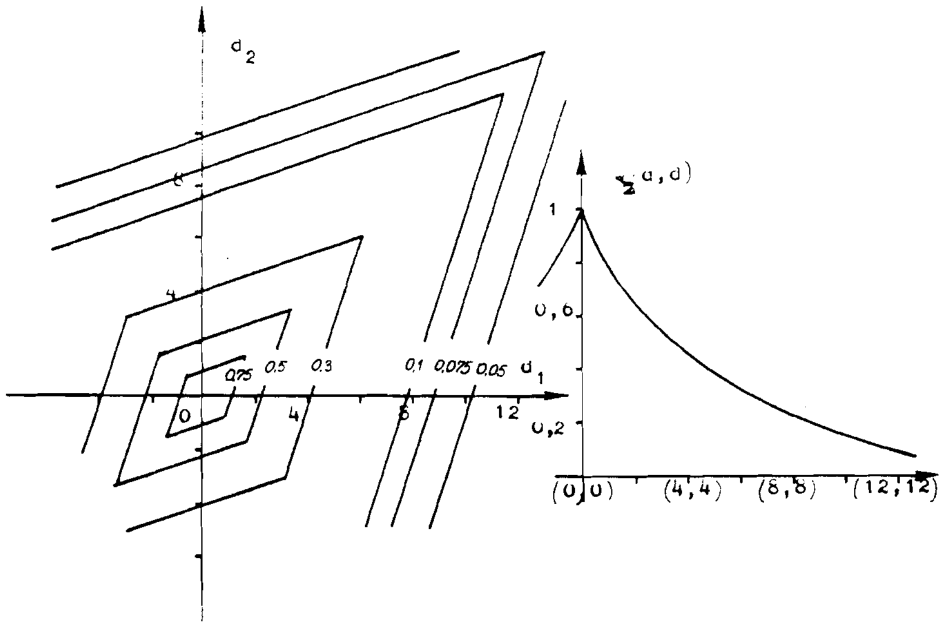

Fig. 5. Map and profile along the ridge of quality function Q_2.

The map of the Q_2 function and its profile along the ridge are shown in Figure 5. All the above functions are rhomboidal shapes, the same profile along the ridges, and a 45-degree tilt to every axis. The better quality along the ridge occurs if two, three, or four parameters, respectively, are simultaneously changed and the improvement is 20%. Changing less than n parameters (n = 2 , 3 , or 4, respectively) leads to worsening the

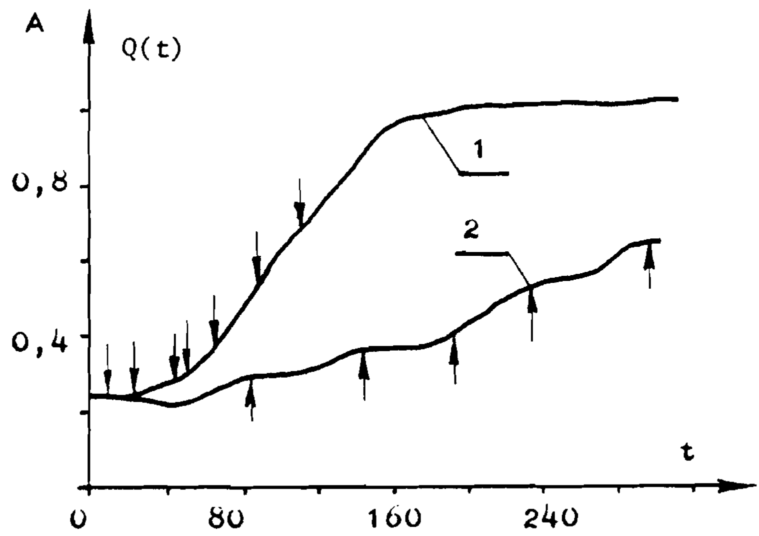

Fig. 6. Average quality in experiments with two- (a), three- (b), and four- (c) dimensional parameter domains and probabilities of modification $p = 5 \cdot 10^{-3}$ (1) and $p = 10^{-3}$ (2).

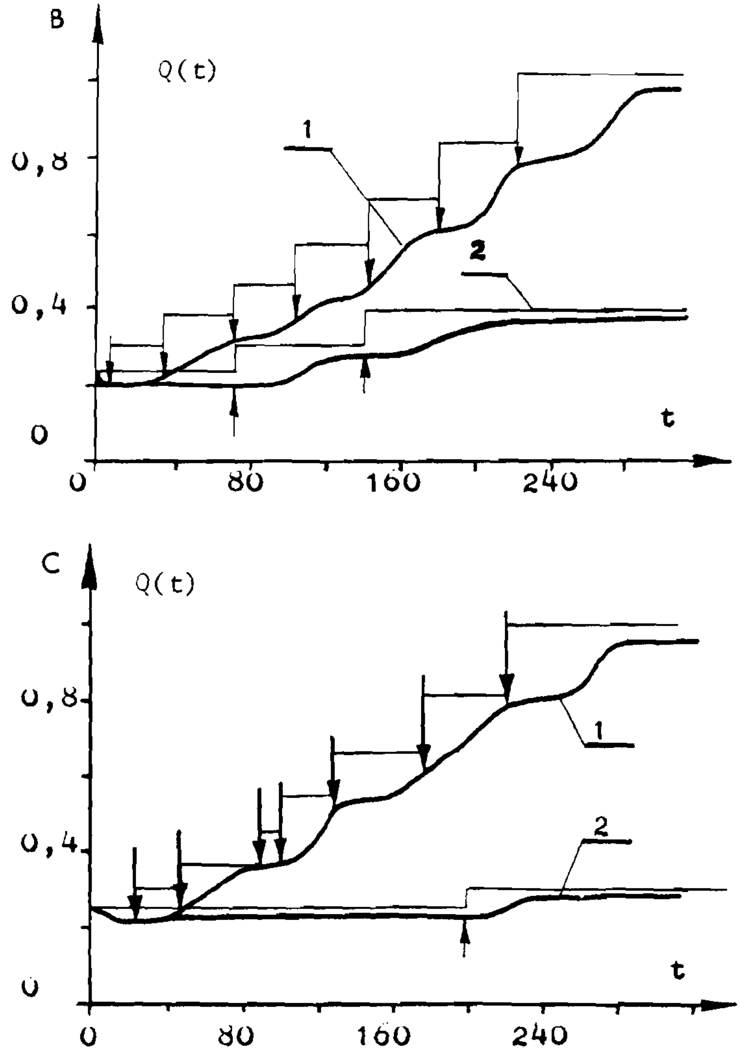

Fig. 6. (Continued)

quality by 4% to 20%. For all experiments the initial population consists of 10^4 elements of types (7 , 7), (7 , 7 , 7), (7 , 7 , 7 , 7), respectively. The average quality in six experiments for two modification probabilities p (10^{-3} and $5 * 10^{-3}$) are traced in Figure 6.

The exemplary d_i parameter distributions at the quasi-equilibrium phase are shown in Figure 7. The distributions look very similar: only a small rise of the dispersion for larger dimensions is visible. If the strongest selection has been assumed (i.e., zero dispersion, with types on the ridge only), then the average values of the waiting time for improvement would be equal to:

for $p = 10^{-3}$	$T = 100$	$T = 10^5$	$T = 10^8$
for $p = 5 * 10^{-3}$	$T = 4$	$T = 800$	$T = 1.6 * 10^5$

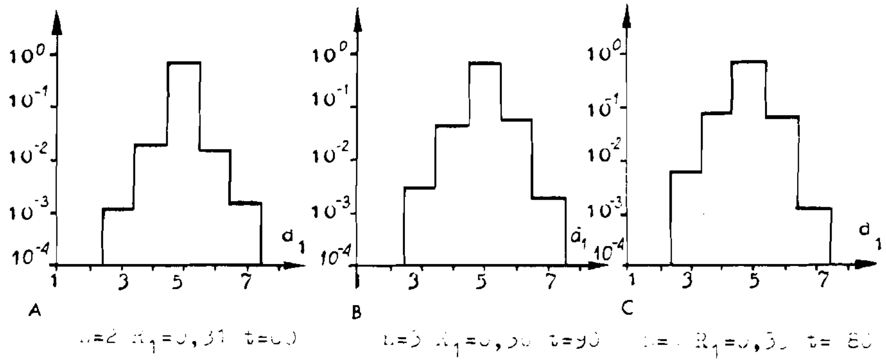

Fig. 7. Parameter distributions of quasi-equilibrium phase for two- (a), three- (b), and four- (c) dimensional parameter domains.

for D^2, D^3, D^4, respectively (the formula $T \approx (p^n * N)^{-1}$ has been applied to the waiting-time reckoning). The expected time of the substitution-phase duration (i.e., the time of growth from 1 element to 10^4 elements) is equal to 50 generations for all experiments. Comparison of the above times with the population development in the six experiments shows an enormous impact of the population diversity on the tempo of evolution. The decrease of the average quality is the price of evolution speed-up; the greater the dimension of the parameter domain, the greater the decrease of the average quality. To expose the importance of the quality discrepancy on the population development, the maximum quality index for experiments with Q_3 and Q_4 are traced also in Figure 6.

II.3. BRANCH POINT

The quality functions in Figure 8 represent the cases of two pathways (chreods) with branch points. For the chreod with greater maximum (Figure 8a) the quality values just after the branch point are smaller than the relevant values for the chreod with a lesser maximum. One may say that the first chreod has a lower initial level of development and better future perspectives in contrast to the second chreod. The initial population was chosen just before the branch point: $N[(13\ ,\ 9)\ ,\ 0]\ =\ 10^4$. The modification probability $p\ =\ 10^{-2}$. Note that 17 times in 20 experiments undertaken, the population developed along the chreod with the lower maximum.

In experiments with two identical branch chreods (Figure 8b) the initial distribution was chosen to provide equal probability of development along these two chreods: $N[(11\ ,\ 10)\ ,\ 0]\ =\ 10^4$; $p\ =\ 10^{-2}$. The population developed 12 times along one chreod and eight times along the second; the case in which a part of the population develops along one chreod and the rest of the population develops along the second one is quite improbable. The parallel development may be caused by isolation of a subpopulation at the right stage of population development.[6]

II.4. THE STABILITY TYPE AND THE MODE OF DEVELOPMENT

All of the experiments presented dealt with the quality functions of the stability type as shown in Figure 9a. According to Waddington [23], the development along these type chreods is very similar for different systems. It seems that previous simulation results correspond with this opinion.

[6]Choosing the right moment of isolation or diverting the system, known in biology as the period of "competence" is discussed by Waddington [23].

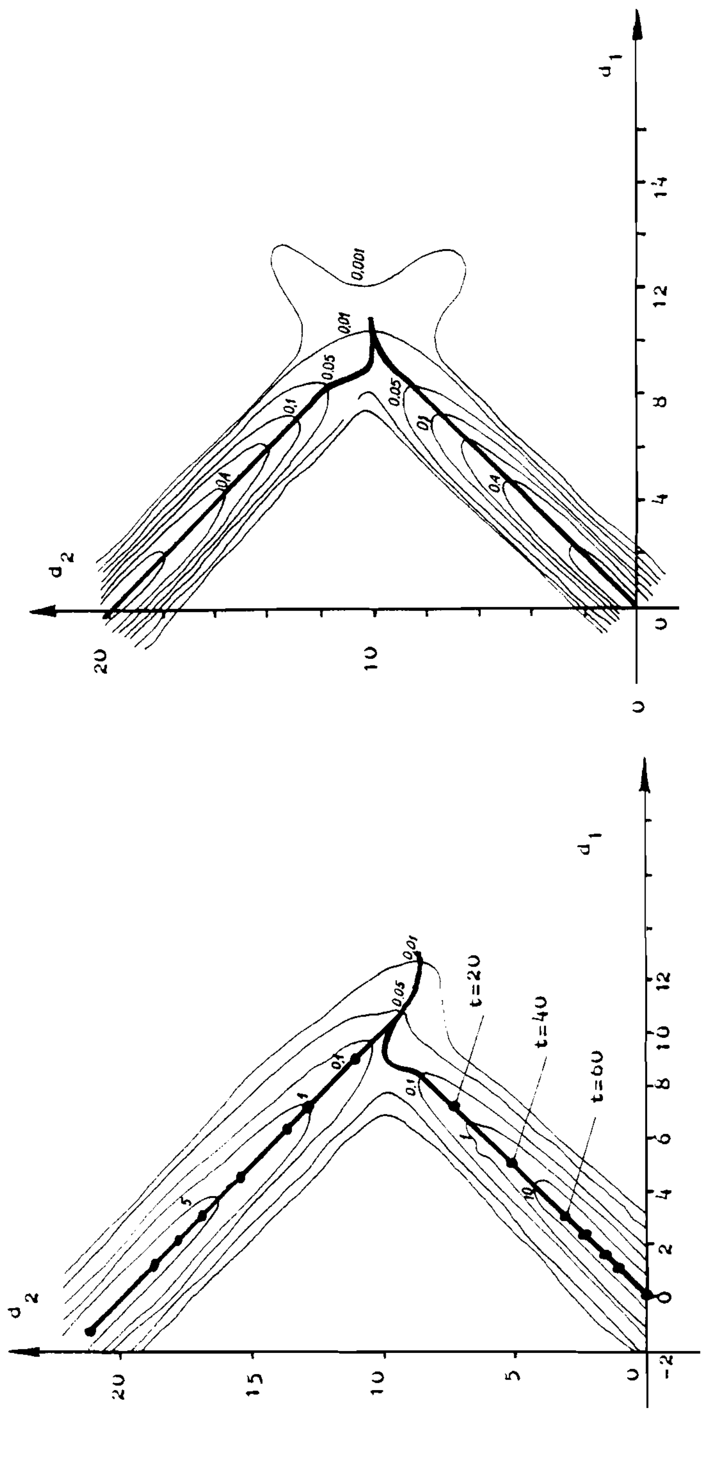

Fig. 8. Development along chreods with branching point.

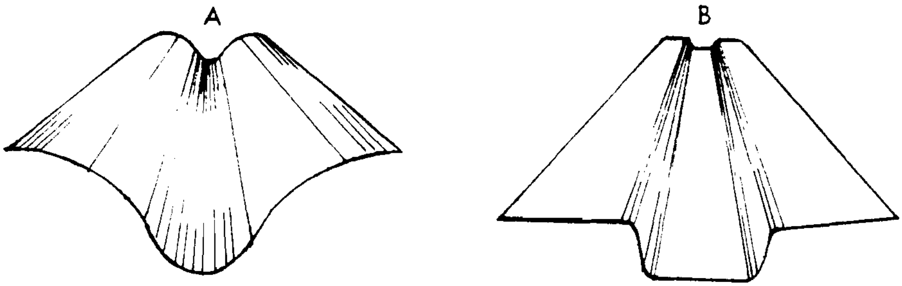

Fig. 9. Chreods with different types of stability, from Waddington [23].

As Waddington points out, the development of different systems along the second type chreods (Figure 9b) are essentially different. Experiments with the quality function

$$Q_5(d_1\ , d_2) = \begin{cases} \mathrm{EXP}[-0.3 \bullet \mathrm{ABS}(d_1 + d_2)] & \text{for } \mathrm{ABS}(d_1 - d_2) >< 5 \\ 0 & \text{for } \mathrm{ABS}(d_1 - d_2) >> 5 \end{cases} \tag{9}$$

are in accordance with this idea. The map of Q_5 is shown in Figure 10, in which five population trajectories with different initial population distributions are traced. Three trajectories (2nd, 3rd, and 4th) start from the same point. The influence of chance on the development trajectories is noticeable.

III. The Rate of Development

The simulation results suggest the essential impact of local shape of the quality function and the modification probability on the population distribution in the parameter domain D^n. From the qualitative viewpoint, the shape of the distribution at the quasi-equilibrium phase is as follows: the population center exists with the bulk of elements and its neighborhood. With growing distance from the center, the number of elements quickly diminishes. Assuming a geometrical distribution of population in D^n seems reasonable. Let us assume that:

1. The population center is at the point with coordinates $(0\ , 0\ , 0\ , \ldots\ , 0) = \mathbf{0}$;
2. No elements of type $(1\ , 1\ , \ldots\ , 1) = \mathbf{1}$ exist;
3. Population is distributed at points $d = (d\ , d\ , \ldots\ , d)$ so that each coordinate d_i may be equal to 1, 0, or -1. That is , $\forall\ i = 1\ , 2\ , \ldots\ , n;\ d_i \in \{1\ , 0\ , -1\}$, and the number of elements of type d is equal to

$$N_d = N \bullet (x^{(n-\|d\|)} \ / \ [(2 + x)^n - 1], \qquad N_1 = 0 \tag{10}$$

where:

N = total population;

n = parameter number (dimension of parameters domain D^n);

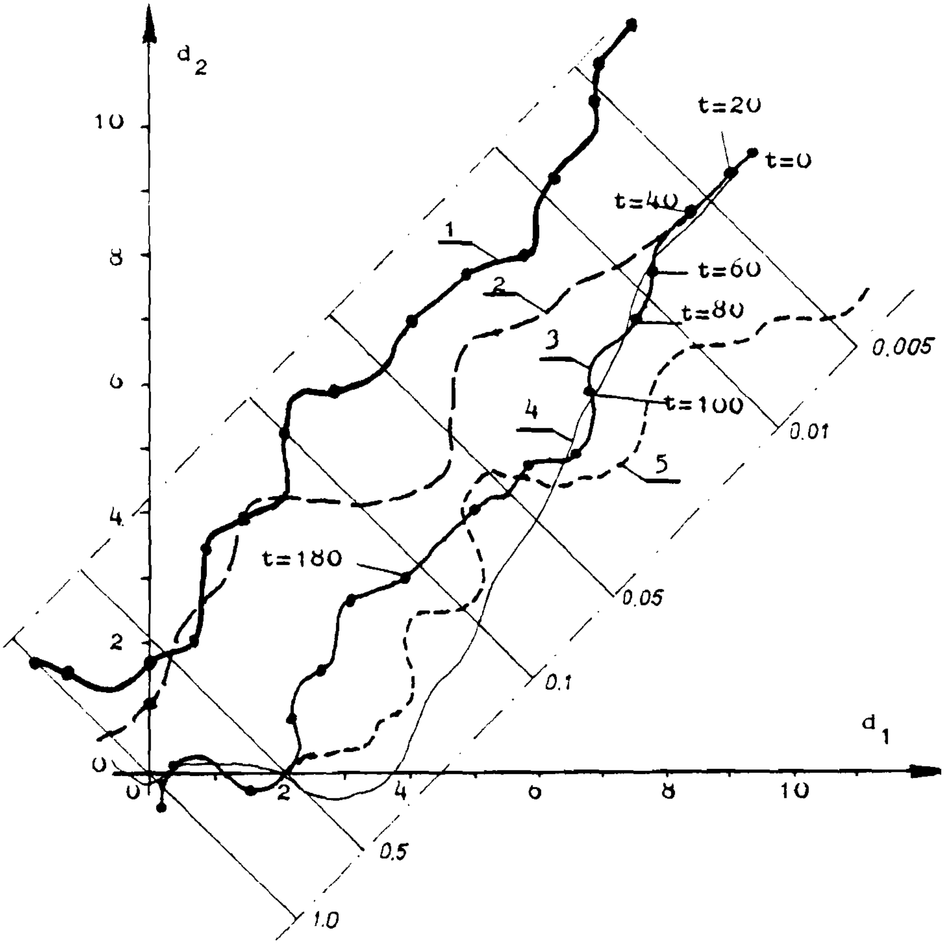

Fig. 10. Second type stability and mode of population development; map of quality function and trajectories of development.

$\|d\|$ = distance of type d from the center (i.e., $\|d\| = \sum_{i=1}^{n} \text{ABS}(d_i')$);

x = distribution parameter.

In other words we assume that:

1. The number of elements diminishes x times in every enlargement of the distance from the center by 1. The expression $x^{(n-\|d\|)} / [(2 + x)^n - 1]$ may be interpreted as the probability of occurrence of type d within the population; and
2. The distribution of each of the n parameters is the same, and the probability that the ith parameter is equal to zero is approximately

$$p_0 = \text{prob}(d_i = 0) = x / (2 + x); \tag{11}$$

the probability that the ith parameter is equal to 1 or -1 is

$$p_1 = \text{prob}(d_i = 1) = \text{prob}(d_i = -1) = 1 / (2 + x). \tag{12}$$

Our interest is the average waiting time for the type **1** occurrence by means of modification of the existing types, under the given population distribution in D^n and given modification probability p (relevant assumptions concerning the modification probability presented at the beginning of the previous section are valid). We consider only modification of types with coordinates 0 or 1 (i.e., $\forall\ i = 1, 2, \ldots, n;\ d_i \in (0, 1)$) to obtain the pessimistic approximation of the waiting time. The probability of occurrence of type **1**, therefore, in one generation is no greater than

$$\begin{aligned} p_1 &= 1 - \left(\sum_{d \in D^n} \{x^{(n-\|d\|)} / [(2 + x)^n - 1] * (1 - p^{(n-\|d\|)})\}^N \right. \\ &\approx N * [(1 + p * x)^n - 1] / [(2 + x)^n - 1]. \end{aligned} \tag{13}$$

For sufficiently great n and small p, the waiting time is approximately equal to

$$T = (1 / P_1) = (1 / N) * [(2 + x)^n - 1] / [(1 + p * x)^n - 1]. \tag{14}$$

Next, let us assume that within the population only types with coordinates equal to 0 or 1 (i.e., -1 is excluded) exist to obtain the optimistic approximation. Making very similar calculations, we find in effect that the waiting time in this case is equal to

$$T^* = (1 / N) * [(1 + x)^n - 1] / [(1 - p * x)^n - 1]. \tag{15}$$

Analogous to Equations (11) and (12), the expressions for the ith parameter distribution in the optimistic approximation have the form:

$$p_0^* = \text{prob}(d_i = 0) = x / (1 + x)$$

and

$$p_1^* = \text{prob}(d_i = 1) = 1/(1 + x).$$

It is more convenient to operate expressions for the waiting time written in terms of probabilities p_1 and p_1^* instead of x

$$T = T_{\max} * (1 - p_1^n) / \{[1 + (p_1 / p) - 2 * p_1] - (p_1 / p)\} \tag{16}$$

$$T^* = T_{\max} * (1 - p_1^*)^n) / \{[1 + (p_1^* / p) - p_1^*) - (p_1^* / p)]\}, \tag{17}$$

Where $T_{\max}$ is the maximum waiting time for a population consisting of type 0 only (zero diversity):

$$T_{\max} = 1 / (N * p^n)$$

The waiting times for $n = 10$ and different modification probabilities are shown in

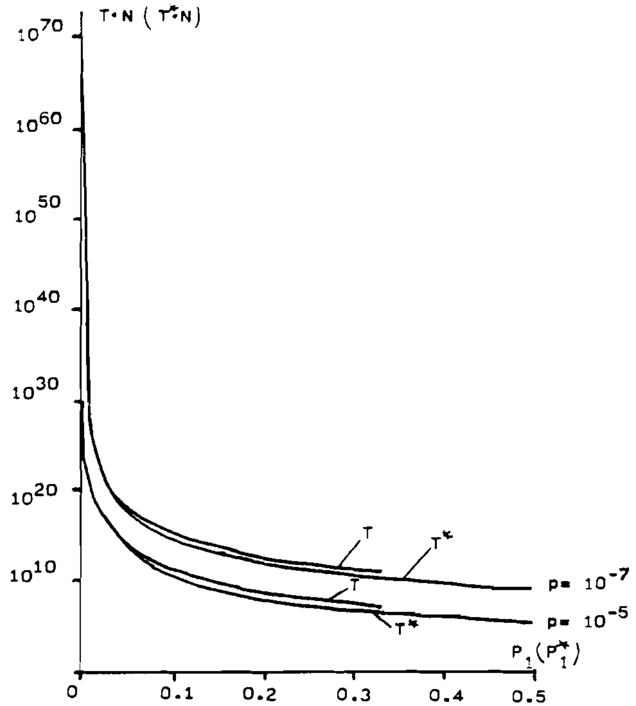

Fig. 11. The waiting time for ten-dimensional parameter domain and for two modification probabilities *p*.

Figure 11. The rapid decrease of the waiting time with growing diversity (especially for small probabilities p_1 and p_1^*) is astounding.

The waiting times, either T or T^*, have an interesting property: namely, the greater the dimension n, the greater the profit flowing from the existence of diversity; i.e., in the sense of

$$\lim_{n \to \infty} (T / T_{max}) = 0. \tag{18}$$

Conclusions

The long-range mode of evolutionary process development is a jerky one, with two successive phases: a quasi-equilibrium phase and a substitution phase. In the quasi-equilibrium phase, two parallel processes act: (1) very noticeably, a gradual (or semi-gradual) improvement process and (2) in the background, a searching process for new basic improvement (that is, improvement the emergence of which radically changes the whole system's structure. In the substitution phase, the new basic improvement supersedes the old one and the system goes to a new quasi-equilibrium. In comparison to the length of time of the quasi-equilibrium phase, the duration of the substitution phase is much shorter and looks like a leap. Duration of the quasi-equilibrium phase is greatly influenced by chance and its probability distribution depends mainly on the population diversity. It is not necessary to postulate intermediate forms between semi-stable forms, observable, for example, in the fossil records; in this context the results obtained are in agreement with Gould and Eldredge's [7] theory of punctuated equilibria.

In addition, the results seem to be consistent with Waddington's ideas of system stability. The course of a system's development (i.e., passing through successive development stages) along chreods with Waddington's first type stability is strongly deterministic. During a system's development, however, short periods in which random factors play an important role occur. They are, for example, the periods just before branch points, development along chreods with Waddington's second type stability. Contrary to "spatial" development, chance influences the temporal system development in an essential way; this is primarily connected with randomness of the quasi-equilibrium phase (random timing of the emergence of basic improvements). Two opposing mechanisms—selection and generation of types—cause the existence of some population distribution within the parameter domain. The distributions consist of the center (containing the best type individuals) and the neighborhood (containing the worst type individuals). The main source of improvements (innovations) is the neighborhood, not, as is commonly believed, the best elements. The existence of the neighborhood diminishes the average quality of the population; that is, it causes a worsening of system performance.

Two main strategies of development exist:

1. Short-sighted: the population is quickly made uniform with the best type elements, making the population more and more homogenous. This improves the system performance very visibly during a comparatively short period. The average quality grows quickly; the uniformization gives spectacular results, but leads to the diminution of population diversity and, as a consequence of this, the probability of basic improvement (innovation) occurrence diminishes considerably. In the end, the system development is much slower; in some cases the stoppage of population development at the actual level (a trapped population) may be observed.
2. Far-sighted: a balanced population diversity exists that makes a worsening of the system performance tolerable and, on the other hand, enables a sufficient rate of development in the long range.

The conclusion that the existence of diversity is of essential importance for long-range system development seems to be intuitively acceptable, but we see strong need of solid verification of this hypothesis. We hope that this verification will be possible at many levels of human activity. Consider as the society a group of scientists engaged in research. Are they likely to be successful if operating as individuals than as an integrated team?

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