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NATURAL SELECTION IN THE EVOLUTION OF HOMINIDS AND ITS RELATION WITH THE FACTORS OF THE HOMINIZATION PROCESS

ABSTRACT. — The relation between natural selection and the defined internal factors of the hominization process is discussed. The authors stress that the concept of the complex of factors as well as the role of natural selection in the human evolution is necessary to develop not on the basis of the clasical concept of an ecosystem but on that of a monotop. Very diverse but relatively stable environmental conditions are presumed in time interval covering hominid evolution. In the concrete realization of qualitative changes and their fixing the natural selection plays a fundamental role by selecting an individual with a concrete type of properties. One is not able to assess the significance of this effect on the structures, which were fundamental for the action of natural selection, and were changing during development of hominid line up to contemporary man.

KEY WORDS: Internal basic factor of hominization — Protoadaptation — Monotop — Active component of adaptation — Natural selection — Plio-Pleistocene hominids — Punctuated equilibrium.

The evolution of Hominids is a complicated process which cannot be explained only on the basis of mechanims of the natural selection. One attempt to solve this problem is the introduction of the so-called internal basic factor of hominization (Vančata and Přívratský, 1978, Vančata et al, 1981a, b). These factors are based on the existence of certain evolutionarily stable morphofunctional structures which have a special significance for the existence of the given hominid form. These factors determine the basic characteristics of the group and the following orientation of the evolution. There are four factors of the process of hominization:

- (I) The factor of bipedal locomotion:
- (II) The factor of the hominid brain and the hand-brain complex;
- (III) The factor of the material culture;
- (IV) The factor of the hominid social organization and the emergence of the human social level.

Let us have a look now at the way of interpretation of the relation between the internal factors of hominization and the environmental conditions and the effect of the natural selection. As has already been mentioned elswhere (Vančata et al, 1981) the factors are based on certain protoadaptations which in a wide variety of ecosystems (e.g. Boaz, 1977, 1979, Butzer, 1978) rendered possible the evolution of specific human features. In speaking about the internal, immanent factors of hominization we therefore have in mind certain morphofunctional units forming the basis of potential adaptations and mutually interacting or interacting with the external conditions of the environment. For several million years these environmental conditions were very diverse (e.g. gallery forest, primeval forest, banks of rivers and lakes, savannas, woodlands, steppes, semiarid and arid regions, highlands and lowlands) but relatively stable. With respect to the wide variability of the environmental conditions

the morphological and functional variability of the hominid material (variability both in space and time) cannot be substantiated by fundamental and sudden changes in the environmental conditions. In our opinion these changes can be explained by a change in the monotop (Schwerdtfeger, 1963) i.e. by a change in some of the various characteristics of concrete ecosystem which might apparently be insignificant for the given form. We therefore do not presume a significant interaction, with all factors of the ecosystem but only with some of them which we denote for the given group as a monotop. A change in the monotop can take place within the framework of one type of the ecosystem. Besides the passive adaptation to the change in the monotop (this is a classical example of the understanding of the function of natural selection) we should also consider the active component of the adaptation to a certain monotop which is closely correlated with the effect, the active reform and the choice of the living environment. The possibility of a choice, i.e. the limits of the active component, are given by the state and the synergism of the internal factors of hominization. In concrete individual this represents a concrete level of development, state and relations between the appropriate morphofunctional complex. This is specifically reflected by the morphology of the fossil material. The concept of the factor is not simply equivalent to the morphofunctional complex of features in a certain living environment. It is an abstract concept and its task is to render possible characterization of the specific features of the hominization process and to differentiate it from other similar processes in primates.

Natural selection determines the appearance and formation of a concrete structure which is a basis of the factor in action. By an elimination of one group of features and by a cumulation of other group the natural selection have participated in fixing the protoadaptations the winning through of which we denoted as factors of hominization. Besides the functional significance the structures have to possess a significant evolutionary stability without which they would not be significant for the existence of the hominization process. However, this does not mean that the structures did not change. The structures were changing with maintaining their basic characteristics which ensured the realization of the given protoadaptations. This is not, however, absolute stability inevitably proper to a given structure only but it is a stability in the framework of the whole organism including its development and evolution.

The effect of natural selection is usually explained on the grounds of a direct interaction between the organism and the living environment (ecosystem). However, in analyzing the concrete cases of effects of the natural selection the solution is incomparably more complicated. We shall try to explain it on an example of the Plio-Pleistocene hominids. At present the basic types of the Plio-Pleistocene hominids are divided into the following groups:

- The ancestral type Australopithecus afarensis.
- The derived types Australopithecus africanus, A. robustus, A. boisei, Homo sp. (cf. habilis)
- The final types Homo modjokertensis, H. erectus.

There is a number of common features between A. afarensis manifesting a number of ancestral features (Johanson and White, 1979, Leakey and Lewin, 1978) and Homo erectus; these common features show that both species pertain to one evolutionary line. The Homo erectus species is already closely related to the Homo sapiens species (especially the younger forms) and differentiation between them is not easy (Jelínek, 1976, 1978). All types of hominids from this period had an efficient bipedal locomotion, a relatively big brain (which further progressively evolved), a developed handbrain complex, the material culture (which was not proved with A. afarensis but which can be expected in its primitive form) and the hominid type of social organization (cf. Isaac, 1980), This indicates that some types of structures of the Plio-Pleistocene hominids were common. These structures were affected by the natural selection in such a way that their relative presentation within the framework of a population increased. Their variability was, due to more intensive selective pressures, less marked than that in number of other structures (morphology of skull, dentition and the upper limb).

The appearance of the above mentioned forms of hominids is usually explained by three types of hypotheses with characteristical factors of the natural selection.

1. The food hypotheses (Robinson, 1972, Jolly, 1970, Szalay, 1975).

The basic selective factors in these hypotheses are the food factors. The food or the way of its obtaining should represent the basic factor of forming the basic hominid structures. These hypotheses have two major shortcomings. They reduce natural selection chiefly to food relations and underestimate the possibilities of food plasticity which is consirable in primates (Firsov, 1976, Chernychev, 1978). The food factors played their role but they do not explain the appearance of the proper food adaptations.

2. The ecological hypotheses (Wolpoff, 1971, Swendlung, 1974, Cachel, 1975, Vančata, 1978). They are based on the presumption of a more or less complex interaction between an organism and the environment. These hypotheses are usually based on general ecological ones. The concept of the natural selection is usually complex but the role of the concrete type of the environment is overestimated. This situation results in an exaggerated stressing of the significance of a certain type of the ecosystem (e.g. the steppe), of the transfers between two types of ecosystems, of a certain type of ecological relation, etc. The role of the natural selection is therefore either underestimated or understood mechanically without considering the active role of the individual in this process. Inspite of the

fact that these studies attempt to form a complex approach to the process of evolution, they cannot explain some important aspects of the hominization

3. The geographical hypotheses (Kortland, 1972, 1974, Geist, 1978). These hypotheses presume an effect of various geographically separated factors of the natural selection on the formation of various types of hominids at least in the beginning of the process itself. In other words they presume a geographical separation of the evolving forms. In many cases this hypothesis is undoubtedly valid. (cf. Kortland, 1972, Geist, 1978) but the fossil finds prove it only partially. It could have played some role especially in the evolution of the species of Homo erectus and Homo sapiens. The hypotheses are based on processes of migration which cause a separation and a sympatrization of forms. However, in some cases these migrations are difficult to imagine (e.g. the East African hominids who lived sympatrically) similarly as some presumed barriers of isolation. In the case of the Plio-Pleistocene hominids it is not very clear why two different forms should exist in two geographical regions which do not differ much from the qualitative point of view. We may deliberate about a converging evolution of two lines of hominids (e.g. robust and gracile australopithecines - Kortland, 1972) but this development in the Plio-Pleistocene hominids is not, due to the considerable morphological simi-

larity, very probable. In summing up we can say about these hypotheses that in most cases they were successfull in explaining up to a certain degree some of the numerous aspects of the hominid evolution; these aspects are explained satisfactorily but the rest of them are not. All of these hypotheses neglect one important aspect of the evolution - the active participation of the individual in the evolution of the hominids. The active role of the individual (including its role in higher units of organization) generates a feedback in the natural selection. In the hominids the prerequisite for the active role of the individual are the protoadaptations (forming the basis of hominization factors) above all the material culture and the social organization (the biosocial factors). The selection of complicated biological and social structures, which are the fundaments of the biosocial factors, cannot be explained on the grounds of few or even a single cause. On the contrary, there was a whole complex of causes which changed during the course of the anthropogenesis. The concept of the complex of factors as well as the role of natural selection in the human evolution cannot be understood on the basis of the classical concept of an ecosystem (the ecotop in this case). It can be understood only on the basis of a monotop, i.e. the specifically generalized environment of the studied form. A limitation of the monotop for various forms of hominids has only to be worked out but there is no doubt that this general ecological concept will elucidate many puzzles in the role of the natural selection in the evolution of the hominids.

The analysis of the relation between natural selection and the internal factors of the process of hominization confirms the justification of the "punctuated equilibrium" theory (Gould and Eldredge, 1977, Eldredge and Gould, 1972, Wood, 1978) and its validity in the evolution of the hominids. A rapid evolutionary shift, the appearance of new forms and rapid establishment of a "equilibrially developing stable system" took place at the moment when the natural selection selected structures different from those, which were the basis for the acting basic internal phyletic factors, or when the formation of other structures began. The qualitative changes took place during the so called evolutionary stress situations no matter whether this stress situation appeared due to the internal changes, the external changes or due to their combined action. In the concrete realization of qualitative changes and their fixing the natural selection plays a fundamental role by selecting an individual with a concrete type of properties. The following action of the natural selection further enforces and molds this complex of properties. It is evident that natural selection played and still plays an important role in the evolution of hominids despite the fact that in many cases we are not able to assess the significance of this effects. The problem is based on the fact that the structures, which were fundamental for the action of the natural selection, kept changing from the individuals with the skeleton suitable for the bipedal locomotion, to the individuals with dispositions to the production of tools and hunting, up to the contemporary man. The action of the natural selection cannot be therefore appraised only globally throughout the whole course of evolution but chiefly in its individual stages.

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