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BIOLOGICAL PREREQUISITES OF THE PROCESS OF HOMINIZATION

ABSTRACTS. — A complex synthetic approach should be the basis for the analysis of biological prerequisites of hominization. There are not only external (ecological) factors fundamental for the evolutionary process but also internal ones defined by the properties of the given systematic unit. The following four main factors of the hominization process have been established: Bipedal locomotion as a locomotor type, hominid type brain and hand brain complex, material culture, and hominid social organization evolving into that of the human society. These factors have a complex character and their intensity changed in the hominization process. A unique interconnection and synergism of the factors led, along with natural selection, to the origin of modern man. For the existence of the factors certain complexes of biological and biosocial features (protoadaptations) are inevitable which can be even common for different factors. We can consider the following ones to be of a special significance: Tendency to non-specialization, polarization and functional differentiation of the limbs, hand-brain complex, tendency to neoteny, hominid reproduction type, tool-making and tool behaviour, and structuralization of the social organization (food sharing, division of labour, prolonged parental care, home base behaviour). The basic factors can not be understood separatelly and as isolated ones; on the contrary, they have to be taken as strictly complex in permanent interactions with external environmental conditions being influenced by the factors of natural selection.

The central problem of the contemporary anthropology is the comprehension of a proper significance of the process of hominization; it is the understanding of this very process which enables us to answer the numerous questions concerning the origin and evolution of the contemporary man and his society. Similarly to the evolution of other species, the process of hominization was a continuous process which linked up with the preceding evolution of a certain group of organisms and took place in a certain environment. The preceding evolution gave rise to certain internal dispositions or protoadaptations which either supported or inhibited further evolution. The conditions of the given environment directed (in a close connection with the internal dispositions) the course of the following evolution. Our study of the process of hominization should therefore be based on the analysis of both the prerequisites, formed by the preceding evolution of the given group of organisms, and on the effective external factors.

The nature of the paleontological material can be studied by two basic methods: the paleoecological and the classical paleontological. The paleontological material, which consists of individual and rare finds and which requires the paleontological approach, renders possible neither reconstruction of the original ecosystem, in which evolution of the hominid took place, nor the concrete prerequisites and the course of their development.

The reconstruction of the process of hominization should be based on a permanent confrontation between the logical prerequisites of this reconstruction (the logics of the hominid evolution and/or of the evolutionary process) and the paleoanthropological findings in recent human populations. Such reconstruction requires a suitable level of generality lest the formed hypotheses should have purely speculative character. This approach permits recognition of the proper elements necessary for reconstruction of the ecosystem, i.e. recognition of external and internal factors of the hominid evolution.

This study uses a relatively high level of generality. We presume certain dynamics of relations between the hominid and the environment, an active role of the ecosystem in the process of hominization and an active role of the hominid itself in the given ecosystem.

The analysis of dynamics of relations between the hominid (or the hominid population) and the environment should be based on a correct comprehension of both the role of the external environment in the hominid evolution and the basic types of its effects on an individual (or population).

The external medium acts on an individual either directly (mutagenetically and morphogenetically — phylogenetically permanent nonhereditary changes and individual nonhereditary changes) or indirectly. The indirect effect of the environment is the basis of the natural selection (Novák and Zemek 1977). However, there is a close connection between the direct and the indirect effect of the environment. At a certain intensity one factor may act selectively (by eliminating some poorly equipped individuals) while at a different intensity its effect may be mutagenetical (i.e. it may bring about nonlethal mutations with a neutral or positive selective value). However, under different conditions the same factor may in a close connection with certain protoadaptations act morphogenetically (by affecting in the so called critical periods the ontogenetical development of each generation it preserves the phylogenetically permanent nonhereditary features). These protoadaptations are usually a product of the preceding effect of the environment (ecosystem).

From the continual character of the evolutionary process follows that methodologically it is useful (and necessary) to separate at a given moment the effect of the environment and the effect of protoadaptations, i.e. the evolutionarily advantageous properties of the given form of hominids.

At the present state of knowledge we are not able to separate the individual simple features which could represent protoadaptations or factors of the hominid evolution.

We shall specify now the most significant complexes of features which became the main complex factors in the process of hominization (Vančata and Přívratský 1978):

1. The achievement of bipedal locomotion as a locomotor type;

2. origin of the hominid type of brain and of the hand-brain complex;

3. origin of the material culture;

4. origin of the human social organization based on the hominid level of social organization.

Each of these factors plays a more or less significant role in the evolution of other recent hominoids and thus it may be supposed that these factors played a role individually also in the evolution of fossil forms. In the evolution of hominids we presume certain balanced at least minimal effect of all of these factors. We should presume that at different stages of hominization the intensity of effect of individual factors varied. What is, however, important is the succession of individual factors. A specific feature is that this sequence holds only in the evolution of hominids and in the following evolution of the genus Homo. A special factor is the social organization, the evolution of which during the process of hominization was a basis for the origin, evolution and interconnection of other factors. It would be wrong to presume that some factors acted separately. It was their mutual interconnection which supported „nonspecialization" and which rendered possible existence in a broad variety of conditions and led to the gradual formation of the contemporary man. This interconnection therefore has a *unique historical character* and its individual components, which we denote as the factors of hominization, are conditioned by each other and are mutually connected. These factors, together with the natural selection, led to the origin of the contemporary man.

We shall not analyze here all the generally known common features of hominids, hominoids and other primates. We shall concentrate only on those protoadaptations which in connection with a given environment played the chief role in the process of hominization and thus made possible the origin of adaptation typical of this process.

The best known general protoadaptation is the preservation of a relatively generalized morphology. The generalized morphology offers a possibility of a high adaptability, plasticity and specialization. For instance, the recent genera Papio, Macaca and Cercopithecus are able to adapt to almost all tropical and subtropical biotops (as shown by a successful introduction of baboons to Caucasus — Chernyshev 1978, Shirinkina — personal communication).

Another important protoadaptation is the polarization of limbs (cf. Vančata in press) which occurs in all hominoids; in hominids it reaches such an assymetry that exclusively hind or lower limbs are used for locomotion. The origin of this protoadaptation may be expected already in the Oligocene forms (e.g. Aegyptopithecus zeuxis) and Miocene forms (e.g. Dryopithecus, Limnopithecus, Pliopithecus and Oreopithecus — Conroy 1976, Szalay and Delson 1979, Strauss 1963).

A shortage of the postcranial material of the first hominids and their closest predecessors renders possible appraisal of neither the evolution of this protoadaptation, nor the origin of bipedal locomotion as a key adaptation of hominids. The character of the available postcranial skeleton of the Pliocene and Miocene hominoids does not exhibit features of an extreme polarization known from the recent apes (a marked morphological similarity with platyrrhine and catarrhine monkeys with polarized limbs can be found). However, due to the above mentioned trend (the generalized morphology) the extreme polarization cannot be expected.

The analysis of relation between morphology and ecology of given forms shows that the morphological "primitivity" ("monkey-likeness") is a very progressive trend. The progressivity may be seen in the "nonspecialization" in the locomotor apparatus which helped the adaptive radiation into the most varied ecosystems (as confirmed by the finds of Miocene and Pliocene hominoids — Pilbeam 1979, Szalay and Delson 1979). The polarization of limbs first led to differentiation of limbs and later to both the different function of the appropriate joints (shoulder, hip, metacarpophalangeal, metatarsopha-

langeal) and the increased disposition to rotate arms and their segments. This proves to be advantageous for obtaining food in different biotops (terminal branch feeding in hominoids, sitting seed eating in the Theropithecus genus). The polarization of limbs is supported up to a certain degree by sitting, which is characteristic for the higher primates. As a resting position it helps the straightening up of the body. However, this posture has no fundamental significance for the evolution of bipedal locomotion, as presumed by Jolly (1970), because it represents an adaptation of one segment of the body without a simultaneous development of other body segments (lower limbs, head, etc.). The development of proper locomotor elements as such was of a basic significance for the origin of bipedality in the process of hominization.

The significance of bipedal locomotion and its selective advantage in the semi-open ecosystems inhabited by hominids is based on higher maneuvering possibilities, on the liberation of upper limbs, on new possibilities of their utilization and on better observational possibilities.

The bipedal locomotion made necessary a number of changes of an adaptative character in other morphofunctional complexes. In brought about changes in the sensoric system, in the embedding of the internal organs, in the position of diaphragm, in changes in haemodynamics, and in a reconstruction of muscle groups connected with the locomotor function. The bipedal locomotion had also effects on the behaviour of hominids.

The most significant role in the process of hominization was played by the origin and development of the hand-brain complex.

The brain, similarly to other organs with a control and regulatory functions, is in a certain sense controlled by organs and systems of a lower organizational level.

The relatively rapid evolution of brain in higher primates is probably connected with the diurnal arboreal life and the necessity of a good spatial orientation, with the evolution of a binocular vision and with the development of certain manipulatory abilities of the upper limb.

There is no reason to presume that at the beginning of the process of hominization the brain significantly differed from that of other hominoids. Due to the evolution of bipedality the fore-limbs were liberated from the locomotor function and part of the brain capacity could have been used for new functions, possibly without increasing the brain capacity. However, the gradual evolution could have led to a situation when the brain capacity used for the development of the new functions of the upper-limb (arm) was exhausted. The hand-brain complex appeared much earlier, before the capacity limit was reached. The substance of the hand-brain complex is not based on improving the manipulatory abilities of the hand alone, but on improving the analysis of the individual's interferences with the ecosystem (feedback) and in the origin and development of association centra which enables synthesis of the obtained information.

The question of the brain size relative increase, which many authors presume (Pilbeam 1980, Campbell 1974, Holloway 1976, 1978, Sacher 1975, Olivier 1973, Wood 1978, Blumenberg 1978), is not sufficiently analyzed due to the shortage of the post-cranial skeleton finds. Nevertheless, we are able to document the absolute growth of the cranial capacity in the Plio-Pleistocene hominids (Wolpoff 1973, Holloway 1976, Tobias 1971, 1975. Le Gross Clark 1962). In the process of hominization both the brain quantitative parameters and the brain shape change resulted in a qualitative improvement of the brain (Holloway 1976). We may say at this point that at the beginning of the process of hominization there existed (from the points of view of the later development towards the man and the possibility of origin and evolution of the hand-brain complex) a relatively efficient brain.

It would not be correct to study the hand-brain complex separately from other mechanisms which led to the brain size increase. An increasing number of data (Roginskyi 1977, Gould 1977) indicates that the evolution of brain is connected with neoteny or a tendency towards neoteny. This question is analyzed in another study (Přívratský 1978, Přívratský et Wierciński in press, Přívratský 1981). The significance of neoteny is based , besides the evolution of brain, on preserving certain degree of universality in the process of hominization. Its existence was made possible also by a relatively long pregnancy and an improved fetus trophics (Doležal et al. 1977, 1978, Hellerová in prep.).

Due to a better intrauterine blood supply of brain than that of other parts of the body during pregnancy an improved development of the nerve tissue (i.e. brain — heterochronia) takes place and results in neoteny. Duration of the human pregnancy is both absolutely and relatively similar to that of the recent pongids. At the same time the human fetus is both absolutely and relatively bigger. On the other hand the morphogenetical development of structures which are not directly essential for life is, in comparison with apes and our predecessors (as seen from the fossil material), retarded (Gould 1977, Pilbeam and Gould 1974). Due to this retardation the development of humans continues after the birth and the final body size is reached in the period of puberty. This fact, together with the general immaturity of the youngs, requires a long period of postnatal care which is closely connected with the development of the human social way of life. The immaturity of brain, which lasts a long time after the birth, proves to be advantageous for a long learning, because stimuli of the external medium act on the immature structures for a relatively long period (Kovács 1960).

This fact opens new possibilities for the development of a differenciated and complex behaviour. The prerequisite for the development of this complex behaviour is a special type of social organization (will be analyzed later).

The evolution of brain, connected with the process of neoteny, depends, besides the internal (proper) dispositions of some forms of hominids, on con-

ditions of the given environment in which these hominids lived.

We may say similarly about the fore-limbs that their development was relatively independent at the beginning. This is due to the fact that the generalized five-fingered limb is typical of primates (Campbell 1974, Le Cross Clark 1962, Chiarelli 1973). However, its use changed in connection with the polarization of limbs and with the verticalization of the posture which in hominids resulted in bipedalism (Vančata 1978, in press). Even a temporary liberation of the upper limb when sitting rendered possible improvement of its manipulatory abilities (Jolly 1970). This is the way how the basic prerequisites for the mutual interconnection of the potential abilities of the brain and the manipulatory abilities of the fore-limb were formed. The formed hand-brain complex achieved, in a close connection with other factors of hominization, high selective values. Thus the hand-brain complex originated in the early stages of the process of hominization.

A necessary prerequisite for the specific function of the hand-brain complex was the achievement of a certain morphophysiological organization of the hand. However, this does not mean that the structure and quality of this hand must have been close to the hand of the contemporary man. From analyses of the tool behaviour of primates and from the studies of fossil material (Beck 1975, Lewis 1977, Thompkins 1977) and the appropriate industries (Isaac 1978, 1980) follows that the level of the hand structure was satisfactory which met the basic demands made on the production of simple tools. After all, not even the hand of the first form of the species Homo sapiens can be compared with the hand of, e.g., the piano virtuoso. The contemporary knowledge on the evolution of hand shows that there is no reason to suppose that in the human evolution situations occurred which forced evolution of the hand comparable with the hand of a contemporary man. It also indicates that the revatively varied possibilities of the hand were, rather than in an improvement of its biomechanical properties, based on the improved possibilities of its control and utilization.

The significance of the complex changed during the process of hominization. The synergic acceleration and intensification of this complex took place only after a mutual action of other factors.

The high selective value of this complex is based on an increase of the behavioural plasticity, which is in the higher animals one of the most important mechanisms of adaptation, and in an improvement of possibilities of active modification of the environment to meet the hominid demands. This fact is further stressed by a close connection of the hand-brain complex with the origin and evolution of the material culture. This culture represents another factor in the hand-brain complex evolution and a new type of behaviour; during the process of hominization it gradually assumed a clean-cut tool character.

However, the material culture is, in contrast to other factors of hominization, considerably more dependent on a concrete ecosystem. On the one hand, the form and quality of the material culture is conditioned by the availibility of the material and realization of possible "technologies" in the given ecosystem. On the other hand, material culture in its development rendered possible decrease of dependence on a given type of ecosystem in which the given form of hominids and their material culture evolved. The material culture made possible interventions into ecosystems which qualitatively and quantitatively exceeded possibilities of biological effects only, and feedback effects of the changed ecosystem emerged.

The evolution of a new type of behaviour and of the material culture is conditioned by an adequate development of the social organization of the hominid life. Certain social structures are also necessary at least so that certain protoadaptations inevitable for the development of the basic factors of hominization can manifest themselves at all (i.e. not only for the preservation of the achieved level of development of other factors of hominization). In a close connection with these factors also accelerates the mutual development of other factors. Similarly with the case of prerequisites of development of other factors of hominization we may claim that the social way of life is a typical feature of primates (with few exceptions) and only a certain type and level of organization becomes the factor of hominization.

In this way we come to another factor of the process of hominization. The social way of life plays a significant role in the process of hominization, firstly, as a precondition for the development of other complexes and, secondly, as a factor which makes possible realization and further development of new possibilities, especially behaviour. How does a certain type of social organization participate in the formation of biological prerequisites of origin of other factors of hominization? Here we shall analyze the question of under which preconditions may the trend towards neotenization, towards prolongation of the period of the postnatal dependence and towards immaturity of the above mentioned brain structures, achieve positive selective values.

The care for the offspring is one of the basic features of social structure and organization of primates. The social organization, however, is not suitable only from the point of view of the care for the young ones. It must be selectively advantageous for the survival in the given environment. What type of organization should therefore be presumed in the protohominid forms?

With respect to the above mentioned connections we must exclude both the solitary family (e.g. gibbon) and the complex and strictly hierarchically arranged big troop (e.g. Papio hamadryas). Such types of socal organization represent adaptations to extreme conditions (from the point of view of the average living environment of primates) which inevitably lead to the limitation of plasticity and universality of the social structure the preservation of which is considered as necessary for the evolution of hominids. In creating models of the hominid

social organization based on the analyses of recent primates (e.g. chimpanzee — Zihlman and Tanner 1978) we should always bear in mind that their social organization necessarily differed from the social organization of the contemporary apes living in roughly the same ecosystem. Certain differences should be presumed in connection with the preservation of a high universality of individuals and of the social organization. This universality is characteristic for the hominid line and its supported by the trend of neotenization which probably represented the basic mechanism of the process of hominization in the shaping of both the biological and biopsychosocial properties. The specialization of the social structure, which is generally necessary for the further development of other structure, was in the evolution of hominids replaced by the origin and evolution of the material culture.

The evolution of the hominid social organization rendered possible and stimulated stabilization of the obtained properties and structural level of a certain group. Together with the tool behaviour and the origin of the material culture it enabled a more effective food gathering, food sharing, the division of labour, and a joint and effective defense against predators in the new ecosystem. A camp was formed. The evolution of the material culture conditioned the origin of a social structure typical of man.

The active part of a given group in the preservation of a dynamic equilibrium in the ecosystem was therefore increased.

As follows from the analysis of the factors of hominization, the evolution of hominids always depended (though not as much as that of a majority of other animal species) on the preservation of a some dynamic equlibrium in the inhabited ecosystem.

The paleoecological studies of localities where fossil remains of hominids were found (e. g. Boaz 1977, 1978, Isaac and McCown 1976) showed that there probably existed more than one type of the inhabited ecosystem. The only common feature was the existence of semi-open ecosystems hominids used to be found either directly in this type of ecosystems or in its vicinity. The hominids probably did not inhabit extreme ecosystems, such as rainforests, lowland forests and deserts.

The approach which we chose in this communication for the analysis of the process of hominization does not allow at the present state of knowledge a detailed analysis of morphofunctional changes or analysis of environmental factors which acted either directly (mutagenetically or morphogenetically), or indirectly in the process of natural selection. However, it enables to perform certain synthesis of our findings from the point of view of the main and decisive forces and phenomena, which played a role in the process leading to the contemporary man, to raise new questions and to give precision to some previously raised ones.

It allows us to select basic complexes of the factors of hominization. Using these complexes we then may appraise the significance of individual protoadaptations for the evolution of the given complex, and, using the relations between the basic complexes (factors), appraise mutual relations of individual protoadaptations in the process of hominization. Only their mutual connection in a certain moment and a certain level of evolution could have led to the contemporary man. There is no doubt that individual factors in different original lines of hominids (according to the concrete factors of the environment and individual mutations and deviations) evolved with different rates. Certain degree of development of some of the main complexes cannot be used as a basis for the appraisal of the achieved level of a certain group of hominids. For instance, only the increase in the brain capacity alone, without an accompanying evolution of the locomotor apparatus and the social structure, need not have led to the contemporary man (and vice versa). This fact is supported also by theoretical findings. Extreme types of ecosystems support formation of either very simple (deserts) or very complicated multilayered (rainforests) relations leading usually to certain types of specialization which we do not expect in the evolution of hominids. The occurrence of hominids in different types of ecosystems does not mean that there did not exist any unifying factor for the evolution of hominids. This factor is the value of protoadaptation of hominids; the protoadaptations were the basis of both the process of hominization and the construction of certain relations in the semi-open ecosystems (i.e. the role of hominids as omnivorous predators which could in the given trend of the hominid evolution exist in a very varied spectrum ecosystems). For the comprehension of evolution of both the hominids and their ecological relations it is advantageous to use the concept of monotops, rather than to analyze in detail and separately relations in the individual ecosystems (cf. Vančata and Přívratský in press b). The biosocial factors started playing the leading role in the ecological relations after the protoadaptations reached certain basic level. Changes in the material culture begun acting as a buffer specific adaptation. These changes were later followed by changes in the social organization.

The global ecological changes, which were necessarilly reflected directly or indirectly in the individual ecosystems, were therefore first followed by changes of biological factors and, after reaching certain level of the evolution of hominids (i.e. after the formation of a consistent material culture), by changes of biosocial factors (these factors became in the following development of hominids the most important ones). The common trend in the evolution of hominids therefore achieved an unifying universal value for different ecosystems of the semi-open character and rendered possible the Plio-Pleistocene radiation of hominids.

The lower rate of the brain development in the groups with a relatively highly developed tool culture and social organization could have been limiting.

The question therefore is as what was the "critical level" of development of a certain complex of

features in relation to other features and as what was the "critical period" for a certain transfer which rendered possible mutual connection of the basic complexes and an acceleration of the evolution.

The approach used in this study permits a more tenacious of purpose seeking of answers to questions about the necessary level of development of certain structures responsible for certain functions, and about the possible effects of environment and its changes, which could have played role in this evolution. Furthermore, in this way we may better appraise many facts which escape direct attention of students in the field of the human evolution.

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