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NEOTENY AND ITS ROLE IN THE PROCESS OF HOMINIZATION

ABSTRACT. — *This communication is analyzing neoteny from the point of view of general morphology and its role in the evolution of man. A new definition of neoteny is presented here and its character is described as an important phenomenon in the process of hominization. The present-day approach to neoteny is compared with the Bolk's theory of fetalization and the main causes of refusing the role of neoteny in the anthropogenesis is explained. Its phylogenetic meaning is emphasised, especially in relation to the function of natural selection. Attention is paid to some neotenic features of the skull, first of all to the findings of the genus *Australopithecus*, and to the role of neoteny in the evolution of the hominid brain. Finally, the relation between neoteny and main hominization factors is considered.*

The work, for the time being, is only a draft of a projected study of a larger extent, which will attempt to assay, within accessible bounds, the part played by neoteny in the process of hominization, i.e. the process which finally led to the formation of contemporary man or, as we sometimes say (with a slight touch of anthropocentrism), modern man. This subject is very ample, linking up a number of biological and anthropological branches of knowledge, yet being elaborated, for the present, only in rough outlines. This complex approach, forced by the subject of research, has its advantage as well as drawbacks. The merits are represented by the ever growing basis of concrete findings and data from individual biological branches, while the drawbacks are based in the fact that not always do we succeed in assaying correctly the significance of these findings in the analyzed general biological phenomenon of an ontogenetic or phylogenetic nature.

In the scientific literature we find occasionally the opinion that for the time being anthropology lacks a sufficient body of data necessary for the formation of reliable theory elucidating or even proving, e.g., such a basic question of hominization like the enlargement of the hominid brain during

the course of its evolution. Olivier (1973), however, expresses this situation very clearly by saying that "... the theories at our disposal do not seem to me to be satisfactory enough to warrant us a performance of general interpretation. Let us wait patiently for a new theory which will be able to elucidate this phenomenon (i.e. the enlargement of brain). For the time being I prefer an observation of facts and give up the attempts to interpret these facts." Olivier thus put a finger on the aching spot of the present anthropology, which not only lacks a sufficient number of concrete information (in contrast with some other, especially the experimental, scientific fields), but also lacks enough good and tenable theories (cf. Pilbeam 1980). My opinion, however, is that those facts which are not utilized in theories or hypotheses lie fallow, preventing us in this way from a correct evaluation of their cognitive significance. Namely, these facts by themselves neither reveal any connections, nor allow us to disprove or substantiate any idea, nor evoke any further effort to reach some understanding; also, they do not allow us to assess further direction of research.

Hominization took place undoubtedly as an

immensely complicated and complex process in which a number of interactions between hominid forms and environment, biological and social laws played part. On the one hand it is therefore correct and inevitable to investigate the process of hominization from the most varying aspects and levels, yet on the other hand we must, now or later, attempt to determine some fundamental, important and decisive phenomena and trends in their historical connections. It seems probable that the very neoteny was the phenomenon which played an important role also in the evolution of hominids, which finally led to the present-day form of man.

In order to be able to perceive and correctly rate its part in the hominization process we should, however, analyze first the concrete content of this term. The concept of neoteny has really underwent a complicated and considerably long historical development. After Karl von Baer, with his ontogenetic rules (K. E. von Baer 1828, 1866), who laid fundamentals to embryology and opened a path to the research of ontogenesis of organisms in the first half of the nineteenth century, then boundlessly increased the number of comparative studies of individual species of animals (vertebrates and invertebrates). On the grounds of information obtained by the comparative method the effort to find and formulate some general laws of the ontogenetic development begins to win through. In 1882 J. Kollmann published a comparative study of some amphibians including the axolotl, and first used the term of "neoteny" to describe that strange state in which this animal reproduces itself and which it differs from the rest of the related forms. Later it turned out that there exists a number of animals which, in their adult age, i.e. according to these studies in the period when they began reproducing themselves, more or less retain the features of their preceding ontogenetic stages. This phenomenon received afterwards a different designation by different authors. It was, e.g., designated as epistasis by Eimer (1890), paedogenesis by von Baer, proterogenesis by Schindewolf (1936), paedomorphosis by Garstang (e.g. 1928), fetalization by Bolk (1926), and bradygenesis by Ivanov (1945). Neoteny is sometimes considered in a more general concept — e.g., in the works of De Beer (1940), who sums up under this term all the above mentioned terms. Neoteny has been studied in a great variety of animals (ranging from invertebrates to man) and plants (Vasilchenko 1965). In practically all these cases the authors dealt with states of the studied objects in which they found some features typical for earlier ontogenetic stages of either the individual proper, or the forms most closely related to it. The merit of these comparative studies of ontogenesis of various organisms is the fact they pointed to various developmental levels of organs or whole bodies of organisms being found on the same or a similar stage of the ontogenetic development. But, as a rule, they did not point to the possible evolutionary significance of these ontogenetic peculiarities. Certain progress in this situation is represented by the later synthetic study of De Beer (1940), who attempted

to bring some rules into the existing chaos in terms, but who similarly mentions the evolutionary significance of the discussed phenomena in a sketchy and vague manner. These problems are dealt with much more consistently, though from a broader angle of view, by Severcov (1929, 1931, 1949) who analyzed and compared various types of ontogenesis and their peculiarities, generalized and assayed their significance in the process of evolution. Severcov finally came to the conclusion (which I consider as being very important and in keeping with the later concepts of the genetic nature of morphogenesis and the relation between genotype and phenotype) that the general fundamentals of these ontogenetic manifestations are, in general, heterochronies, i.e. the successive time changes of individual ontogenetic processes. Severcov himself divided these changes into two groups, i.e. accelerations and retardations. Later, on the grounds of a concrete research, this division was further redefined (Novák 1960, Novák and Přivratský 1978).

The above mentioned original studies concentrated therefore on the ontogenesis of contemporary and more or less related (or similar) forms without taking into consideration their historic development and, consequently, some significant chains of events. This approach leads inevitably to an extensive schematization and mechanistic descriptive standpoint. In the main, neoteny is a designation for either the phenomenon in which the studied organisms exhibit (in the beginning of their reproductive period) features of their preceding stages or similar stages of related forms, or the phenomenon in which properties of a young individual of an ancestral form appear in adult individuals of a descendant (De Beer 1940), the relative retardation of body development with respect to reproductive tissues being taken into consideration in the same time. A positive feature of the latter case is the very presence of phylogenetic standpoint, because this standpoint allows us to assay neoteny as a phylogenetic, *evolutionary phenomenon*. The shortcoming of this formulation is, however, the consideration of neoteny on the grounds of relation between the degree of somatic development at the maturing age and the complex functional activity of both the reproduction tissue and the reproduction organs. Though it is possible and probable that inhibition or slowing-down of the morphogenetic process takes place as the consequence of initiation of a complex physiological function of the reproductive tissue, the process need not be necessarily terminated. In this way the beginning of reproduction becomes the stage in ontogenesis which might be important for assaying the acceleration of the development of individual structures on the grounds of the state of these structures in this stage; the stage renders information about neither the final morphological shape of the individual features or even the whole organism, nor about the degree to which neoteny (in the sense of the above definition) in its final shape (or function), i.e. at the termination of the morphogenetic process, comes to function. Consequently, neoteny could be, or need not be, connected with retardation. Similar abuses or logical

inconsistencies could be met with also in the deliberations about the part played by neoteny in the evolution of man. The "fixed point in space" is, in this case, the birth of an individual, to which the morphological state of the newly-born human is related. The phenomenon dealt with is thus neoteny, because the human at birth is "immature", retarded and not yet fully developed in comparison with other primates; yet its morphological state (more precisely the morphological state of its concrete features, i.e., structures and, possibly, also functions) at the time of termination of the morphogenetic process is not taken into consideration. From the reasoning given above follows that acceleration or retardation themselves do not yield information about neoteny, if the studied stage is not compared with the final morphological shape of an ancestor (primarily). If relatively identical ontogenetic stages or phases of close forms of organisms are studied, then the terms of acceleration and retardation are suitable concepts to express the type of heterochrony. In order to formulate the concept of neoteny correctly we need to settle necessarily two important questions. On the one hand it is the question of termination of the morphological process, and on the other hand the question which organisms we are justified to compare, and up to what degree.

The concept of "morphogenesis" (morphogenetic process) serves to express the progressive development of shape, i.e. the process in which at any time there exists a state with prevailing constructive (anabolic) processes, the destructive (catabolic) processes being represented to a lesser degree. The morphogenetic process terminates by reaching an equilibrium (dynamic equilibrium), after which the shape stabilizes and the corresponding structures (i.e. organs) fulfill their function for a certain time. The morphogenetic process is thus independent of both the period terminated by the maturity of the reproduction tissues, and, in the case of man, of the prenatal stage.

The second question is even more complicated. Namely, it is connected with a whole set of problems, as, e.g., the relations between phylogenesis and ontogenesis, genotype and phenotype, effect of the external environment on morphogenesis, etc. The comparative method, used in biology since its beginnings, certainly renders the research invaluable services and is very useful up to the present day. The method could, however, lead to mechanical conclusions, which are often totally false, because they are based on an incorrect presumption of adequacy of the compared structures, functions or phenomena in general.

Let us study this problem from the standpoint of evolutionary anthropology. It is quite common in the anthropological literature to compare modern pongids with fossil forms of predecessors of man. In comparing the cranial capacity of fossil hominids Olivier (1973), e.g., substitutes the cranial capacity of Ramapithecus (the estimation of this capacity still remains, as a matter of fact, very questionable due to the shortage of an adequate skeletal material)

with the cranial capacity of chimpanzee. However, the presumption is at least hypothetical and applicable perhaps for an appropriate illustration of the enlargement of the cranial capacity during the course of hominization. On the other hand this comparison brings about an ill-founded and unsubstantiated belief that the older hominid forms are the more their morphology resembles that of the modern apes. A false conclusion follows that for this reason it is quite possible to draw conclusions from the comparison of modern forms (e.g. the present-day man and chimpanzee) without bothering with a closer specification of their mutual phylogenetic relations. Man is thus attributed certain evolutionary changes at the expense of the phylogenetic evolution of apes. At the same time it is clear that the present-day living pongids have passed through a relatively long historic development and are modern, too; i.e. similarly to man they are just the contemporary forms and their evolution evidently continues (as we shall see on the case of bonobo — *Pan paniscus*). We may compare and may possibly draw evolutionary conclusions from these comparative studies, but only if we know the phylogenetic development and the phylogenetic relations of the compared features. In the case of phylogenesis of apes we are, for the time being, handicapped by the almost total lack of concrete fossil material. Despite this fact (or rather just due to this fact) the first theories about neoteny in man appeared on the grounds of comparison of the ontogenetic evolution of man and the apes (as well as other mammals e.g., dog), especially of their fetal and postnatal periods. In 1926 Bolk published a work in which he substantiated his theory of fetalization in man with the aid of retention of morphogenesis of a number of morphological structures at the fetal period level (Devaux published the same theory in 1933). The most important neotenic features are the relatively high weight of the brain, position of the foramen magnum, the so called cranial flexure, the very retarded closing of the cranial sutures, dentition, orthognath, naked skin, light colour of the skin, increased retention of cartilage as well as some other features. From this specification it is evident that Bolk mixed up some solid proofs of neoteny with some more or less unwarranted assertions to which he came chiefly due to the fact that he mechanically formed conclusions on the grounds of one-sided comparison of an early ontogenesis of apes and man. His mistakes were used (unfortunately quite successfully) for quite a long period by the opponents of the idea of participation of neoteny on the phylogenetic development of man. Even today it is very difficult to verify this idea despite the fact that we have at our disposal a considerably higher amount of concrete findings and data from a number of biological fields.

Presuming that we may rely on the fossil skeletal finds it is evident Bolk's guesses were correct (more or less). It is first of all the relative increase in the cranial capacity and, so in the brain size during the process of hominization. Significant is also the position of foramen magnum despite the fact that this position is related to the evolution of

the locomotion mode. This should be true because heterochrony of the progressive retardation type led to the neotenic fixing of the position of this opening, making thus possible (naturally in a feedback) the appearance of bipedalism or, in other words, it was one of its necessary conditions. The concept of cranial flexure is rather a schematic one. In reality, no clear flexure takes place in the fetuses of the quadrupedal mammals; on the contrary, individual structures of the rear of the head grow at different rates, so that as a consequence the organs of sight assume the appropriate position on the frontal part of the head. In this place we come upon another Bolk's inconsistency: he demonstrates the cranial flexure on the evolution of dog, i.e., compares man with a quadrupedal nonprimate. Dog has a different course of morphogenesis as compared with man and the verification of neoteny in different genera by making comparisons of this kind is questionable. Besides that the cranial flexure must take place in ontogenesis of all animals which use for locomotion two limbs and whose body axis is oriented more or less vertically. The modern apes undoubtedly belong to this group of animals; their eyes assume the same position as the man's ones. The cranial sutures in man obliterate very late (as a rule not before the thirteenth year of age), sometimes even at a very advanced age or not at all. We find the unclosed cranial junctures also in the fossil material of the man's ancestors, but the phylogenetically older is the fossil material, the more rare is their occurrence (unless the fossil remains of a juvenile individual are taken into account). Considering the fact that the sutures obliterate (if they obliterate at all) only after the form development has been terminated, we are allowed to make conclusions about the demonstration of neoteny from the comparison with man's ancestors or even the apes. A similar situation is with the relatively higher level of cartilaginous ligaments retained to the adult age; the assertion, on the other hand, that the white human race is more neotenic than the black one (because the melanine pigment is synthesized only after a birth) is at least unprecise and exaggerated (are the differently pigmented ethnic groups differently neotenic?). Besides that, two human races are subjected to comparison from which follows the conclusion that even if the two races were differently neotenic, the neoteny of this feature is not important from the point of view of hominization. Yet our task is to study its evolutionary mission, because neoteny is significant chiefly as an evolutionary mechanism, i.e. the mechanism which played an important role during the process of hominization. It was the basis for some modifications — e.g. the brain size, immaturity of man's offspring, etc. These changes finally made themselves useful as the decisive factors of hominization (Vančata and Přivratský in press).

In the first part of the introduction we discussed the question of acceleration and retardation and stressed that these phenomena need not necessarily be connected with neoteny. In order to explain these phenomena by neoteny we need, besides finding retardations of some structures or the organism

as a whole (e.g. at birth or in the period of sexual maturing), to know the state of its structures in the end of the morphogenetic process and we must compare this state with the terminated morphogenesis of the adequate structures of the ancestors. Comparison of the studied organism with some other modern organism may serve as the first indicator calling our attention to the possibility of participation of neoteny in the phylogenetic evolution of the studied organism. Yet it is true only when the genera are positively related and their mutual phylogenetic relations are known to us. It was just this important circumstance which Bolk either did not recognize or simply did not take into consideration. In accordance with the dogma of that time he automatically presumed that the modern pongids as a whole represent the form from which the modern man evolved. And it was just this problem of comparison adequacy which represented the weak point of the formulation of neoteny in the process of hominization (e.g. Bolk, on the one hand, compares man to dog in the case of demonstration of cranial flexure, and, on the other hand, compares modern man with a modern man in the case of demonstration of the light and the dark skin, i.e. two variants of the same species). There are, however, authors who have been refusing or still refuse to consider neoteny in man, because they, for some reason, did not understand or did not want to understand its progressive character in the general evolution of man; on the contrary, they presumed that we deal essentially with a regressive retardation, i.e. some sort of return to the primitive state, and tried to prove that neoteny did not take part in the evolution of man. They considered various adaptations which are not at variance with neoteny (on the contrary, neoteny may even result from these adaptations). The authors were not simply able to put retardation in connection with the progressive evolution. They did not recognize that it was just this connection which served as a source of new characteristic features of man. They did not notice that the loss of some end stages of morphogeny occurring in man's ancestors opened new possibilities of adaptations (Starck 1962, Starck and Kummer 1962, Schindewolf 1972).

In summarizing this partial analysis of the concept of neoteny we may attempt to draw its new and more precise formulation. *As neoteny we may consider that phylogenetic phenomenon which is based on ontogenetic heterochronies of the progressive retardation type and in which some features or properties of the adult organism or possibly the adult organism as a whole (e.g. the male individual of the Bonellia viridis species) exhibit properties characteristic of the same features (including the functions) of the ancestors which are found at earlier morphogenetic stages than the progeny.* Neoteny, being a phylogenetic mechanism, represents an important evolutionary factor. Its evolutionary significance is chiefly based on the fact that new features of sometimes high selective value appear through the mediation of neoteny. Neoteny represents, in other words, a significant adaptive means

which makes itself useful through the agency of natural selection.

Simpson (1969) in connection with this problem rightly remarks that though the de Beer's survey or classification of different ontogenetic morphogenetic processes is exhaustive and certainly also useful for the description of some features of the comparative embryology, it fails to explain the cause due to which these ontogenetic systems became different. The survey yields no information about, e.g., the character of neoteny of echinoderms leading to the formation of chordates: rapid, sudden or gradual, whether it was caused, according to Simpson, by a single mutation or one million mutations.

There is practically nothing known about the genetic nature of neoteny. Some authors presume that similar processes are conditioned by mutation of just very few genes which control the growth (Weiss and Maruyama 1976); similar conclusions in connection with the brain expansion during the process of hominization were reached by Kimura (1960). According to our presumption (Přivratský 1978) a basis of neoteny may be originally just a single simple mutation, which could cause a change at the beginning, in, e.g., the intensity of the effect, and in the level of production of certain morphogenetic hormone (e.g. the growth hormone). This mutation would not naturally manifest itself in the phenotype automatically; on the contrary, its manifestation is dependent on a number of interactions with other genes and mutations as well as factors of the external environment. This coupling with the living environment may be so strong that neoteny may ensue from a mutation which appeared in the genotype much earlier, but which comes into prominence only in a certain evolutionary situation, in a later stage of the phylogenetic evolution of the species. Neoteny than maintains its level (i.e. passes from one generation to the following one) as long as continue the environmental conditions (within the framework of the variation interval) admissible for its maintenance. Neoteny is, in other words, maintained by morphogenetic factors of the environment (which simultaneously represent, in this case, the selection factors) and is thus of a nonhereditary phylogenetic character (Zemek and Novák 1977).

Some researchers still believe that neoteny is essentially a delay or retention of the general development of an organism in the early stage of ontogenesis which plays part in the ontogenesis of a species. Such a point of view is a little simplified, though in certain cases it may be true. The evolution of hominids, however, takes place in a mosaic manner, i.e., some features and structures are not of the neotenic but rather of an conservative character. They are common to all hominoids and primates and therefore to man's ancestors, too. At the same time every hominid, as we may judge from the present-day available fossil material, represents a characteristic mosaic of properties, some of which manifest themselves relatively early (at the beginning of hominization process), while others (or the same ones again) occur in evolutionarily younger forms. Indeed, this mosaic of neotenic features

forms a homogeneous entity with other properties of an organism. The process of natural selection then modelled those forms which, at the given stage of evolution, suited best the conditions of the external environment.

The evolution of man is, similarly to the evolution of other species, a historic process. In order to assay correctly the part played by neoteny in this process we should utilize consistently the findings about the actual phylogenetic relations; it was just the poor understanding of these relations which led to ideas which are too hypothetic and rash. Ideas of this kind slow down, rather than accelerate, the process of discovering. It is, therefore, necessary to draw careful conclusions utilizing as much concrete data and fossil as well as comparative material as possible.

Let us have a look at several concrete examples interpreted as proofs of role of neoteny, as they were gradually brought forward by the paleontologic research.

SOME NEOTENIC FEATURES OF THE SKULL

The paleontological research increased the amount of fossil material to such a degree that we face an ever improving and very important opportunity to assay the manifestation of neoteny in the hominid line on a concrete skeletal material. Also the amount of finds of skeletons of juvenile individuals increases. In an overwhelming majority of cases these are bigger or smaller parts of the cranium. We shall have a look at several forms and attempt to interpret their morphology in terms of our concept.

It is not a long time ago that remainders of a form lying on a boundary between the genera Australopithecus and Homo and labeled as SK-27 and SK-47 were discovered in Swartkrans in south Africa. These finds were originally qualified as the robust forms (Paranthropus); today, however, they are, on the grounds of some features, qualified rather as the early forms of the genus Homo (e.g. the mutual position of glabella and nasion). Very interesting area is, for example, around the mastoid process. Both the finds, SK-27 and SK-47, show a well developed mastoid notch (digastric groove). This notch runs through the middle of the mastoid process and is separated from occipitomastoid suture and from the groove for the occipital artery (arteria occipitalis) by a prominent occipitomastoid crest. The morphological similarity of SK-27, SK-47 and SK-847 is of a neotenic character (which is described and considered in the American literature as the so called synapomorphic character of these finds, Olson 1978), which differentiates this similarity from the symplesiomorphic situation typical for Paranthropi and all the present-day pongids. In the present-day pongids, m. digastricus exhibits a nonlinear ovoid rough origin on the medial surface of the occipitomastoid crest located immediately laterally to

the groove for the occipital artery. This crest separates the medial border of the digastric fossa from the lateral margin of the depression where *m. obliquus superior* begins. Similarly with the crest runs the occipitomastoid suture which provides support for this muscle. *Paranthropus boisei* (O.H.5) exhibits, in contrast with the mentioned finds (i.e. SK-27, SK-47, SK-847), a conspicuous spur on the left (preserved) surface of the nuchal planum, which is a constituent of the interior nuchal line (Tobias 1967). In the modern man the structure separates in this region the sites of origin of muscles *m. obliquus superior* and *m. rectus capitis posterior major*. The O.H.5 find exhibits immediately laterally from the spur a depression which can be best interpreted as a place for the attachment of *m. obliquus superior*. The morphological differences in this region between the *Paranthropi* and the *Australopithecines* were described by, e.g. Olson (1978), who compared the detailed anatomic descriptions of other finds (KNM-ER-407 from the Lake Rudolf, today Turkana, and TM-1517a from the finding locality Kromdraai in South Africa — it is the only find of *Paranthropus* in this part of Africa) and detected some common primitive relations between the occipitomastoid crest, the groove for *arteria occipitalis* and the place for attachment of the digastric muscle in these forms and the O.H.5 find. The neotenic character of the position of fossa digastrica and the mentioned structures of this region of cranium (including suture occipitomastoidea) phylogenetically differentiates SK-27, SK-47 and SK-847 from the rest of *Paranthropines* and qualifies them to MLD 37/38 from Makapansgat, Sts-5 from Sterkfontein and the later hominids (e.g. Sangiran IV or Peking XI). It seems very probable that from the evolutionary point of view the phylogenetically more advanced character of the mentioned structures acquired these forms (in contrast to *paranthropines*) from the ontogenetically juvenile and morphogenetically earlier stage of the same structures in the succession of ancestors — i.e. by the means of neoteny.

A further concrete proof of the cranial neoteny in hominids are the features of substantial parts of the SK-27 and SK-47 fragments evident from the occipital view. For instance, in both these finds the mastoid processes are represented by small pyramid-like structures bent in the direction under the cranium. From the point of view of higher hominid it is a "primitive" or neotenic feature in contrast to the also "primitive" (from the point of view of evolution of man), but a specialized feature represented by the great supramastoid crest and tilted temporal squama. The lateral surface of the mastoid process goes relatively smoothly into an almost vertical temporal squama which has only a small supramastoid crest. This is also a feature which differentiates both of these finds from the specialized form of *Paranthropus robustus*, in which the mastoid process is inflated laterally and inferiorly from the cranium (c.f. TM-1517 from Kromdraai, the incomplete cranium SK-52 and SK-79 from Swartkrans). The increased mastoid process together with

the strong supramastoid crests and more steeply slanting temporal squama give the crania of *paranthropines* their characteristic outline. This trend reaches its extremity within the range of *Australopithecus boisei*. Further research showed that the given set of features has a considerable diagnostic significance. With the help of East Turkana finds (two small crania of *Paranthropus robustus* KNM-ER-732 from Koobi Fora, Area 10, published by Leakey, Mungai and Walker 1972) it became evident that the characteristic development of this complex of characters is independent of the individual size: both crania, most probably female, have the mastoid process and the supramastoid crest (crista supramastoidea) just a little more robust than the male cranium (e.g. KNM-ER-406 or O.H.5). In some cases the cranial neoteny played a role only in the case of mastoid process, while the supramastoid crest remains prominent. This feature occurred, e.g., in the SK-847 find which resembles the MLD 37/38 finds in its structure of the mastoid region. It is just the morphology of this region in SK-847 that serves as a conclusive argument against the opinion that differences between these structures in *paranthropines* and the other hominid forms occurring on the boundary between the *australopithecines* and man have an ontogenetic rather than phylogenetic character. We thus reach a conclusion that from all the mentioned features (a small bent mastoid process, a large supramastoid crest, a slanted temporal squama) occurring in the more advanced hominids neoteny played a part only in the case of the mastoid process. The neotenization tendency has been gradually gaining strength during hominization process and it affected also some other structures in this region of the cranium (disappearing of the supramastoid crest, retention of more vertical position of the temporal squama in the more advanced forms during hominization process).

In 1978 Rak and Howell described the cranium of a juvenile individual of the *Australopithecus* (*Paranthropus*) *boisei* 2.1 million years old (L 338-6, found in the Shungura Formation from the basin of the lower Omo river in Ethiopia). They claimed that its general resemblance to gracile *australopithecines* was chiefly due to the youth of the individual. Certain morphological features of this cranium bear resemblance even to the morphology of modern man (the angle between occipital condyles, width-length index of foramen magnum etc.). Our conviction that the evidence of neoteny in man need not be backed any more by comparative material of the present-day pongids (as we have now at our disposal some data concerning directly individual members of the hominid succession) thus proves to be correct. On the grounds of the Schultz method (Schultz 1962) utilized according to Enlow (1968) is possible to calculate the postjuvenile change. This change is expressed as a percentage of the juvenile value. If, e.g., the juvenile value of the given dimension is 100 and the adult value is 120, the difference is 20 and the postjuvenile change is equal to 20 : 1, i.e. to 20 %. The total change is then represented by the mean value of all the measured

postjuvenile changes. It was calculated that the total postjuvenile change in the morphology of cranium of *A. boisei* equals to 23.7 %, in chimpanzee to 16.34 percent, while in man this mean value represents only 5.78 % (Rak and Howell 1978)!

Furthermore, the juvenile individual of *A. boisei* L338-6 from Omo exhibits a relatively thin and flat pars basilaris ossis occipitalis in contrast to the adult individuals in which this part is relatively massive (e.g. O.H.5 and KNM-ER-406); as far as the robustness or massivity of pars basilaris are concerned, in man these relations are similar to those of the L338y-6 find. Also this example shows then that there was a trend in the phylogenetic succession of man to gradual gracilization, which was reached by the development of individual features or structures from conditions typical for earlier morphogenetic stages of ancestor's ontogenesis.

There is a very interesting finding that as far as the changes of proportions of basal part of the occipital bone are concerned, the relations in the *Australopithecus boisei* (finds O.H.5 and the juvenile cranium L338y-6), expressed by the basis occipital index

$$\frac{\text{width of the basal part of the occipital bone}}{\text{length of the basal part of the occipital bone}} \cdot 100,$$

are very similar to those in the present-day man, as the change of this index between the juvenile and the adult individual is similarly small as in *Homo sapiens* (the L338y-6 index equals 106.3, the O.H.5 to 110.5, the present-day juvenile man index equals 87.9, the present-day adult man index equals 100.0; c.f. also a table in Rak and Howell 1978, page 354). On the other hand a substantial lengthening of the basal part of the occipital bone during the development and maturation was found in chimpanzees and gorillas (the index equals in the juvenile chimpanzees 82.8 in adult chimpanzees 66.8, in juvenile gorillas 73.9 and in adult gorillas 62.6). This lengthening of the basioccipital part of the cranium is attributed, e.g. by Schultz (1962), to major ontogenetic changes of the dimension of basion-prosthion or, as mentioned by Ashton (1957), to the changes in the middle segment of the basicranial axis. The fact that pars basilaris ossis occipitalis remains short in *A. boisei* (similar to man) points at the connection between the manifestation of neoteny in this feature and bipedal locomotion. Besides that, the presumption of the mosaic role of neoteny in the process of hominization is again verified.

If we, on the other hand, compare the position of the occipital condyles with regard to the foramen magnum ossis occipitalis we find that the condyles in the L338y-6 juvenile individual (similar to present-day man) do not reach the front border of the occipital bone (the distance between the front border of condylas and the front border of the occipital bone equals to 3 mm), while in O.H.5, i.e. in an adult *australopithecus*, the front border of the condylas extends beyond the front border of the occipital bone by 7 mm. This feature is even more marked in the KNM-ER-406 find (Rak and Howell 1978). A conclusion follows from the above men-

tioned facts that there are relatively big morphological differences between the juvenile and the adult *australopithecines*. The bigger and the more significant are these differences, the more marked was the role played by the phylogenetic mechanism of neoteny during the course of hominization.

Unfortunately, there is practically a total lack of fossil material from the phyletic succession of chimpanzees and gorillas. Though (as already mentioned in the preceding theoretical part) it is very difficult to assess the phylogenetic manifestation of neoteny in man or pongids by comparing the ontogenetic development of man with that of pongid it would certainly be very interesting to determine the appropriate cranial neoteny in the evolution of pongids and compare it with cranial neoteny in the hominid succession. At present we are not able to judge whether the individual morphological features of the modern pongids are or not the manifestation of neoteny, and if they are, then to which degree. If, however, this appreciation is possible in the future (i.e. when we shall have at our disposal a sufficient amount of fossil material from the phyletic succession of pongids), we might be licensed to utilize the modern pongids for a comparative proof of neoteny in the present-day man in a far greater extent than today without committing bigger inaccuracies or mistakes.

As far as the apes are concerned, several recent studies differentiate between the *Pan paniscus* chimpanzee species and the *Pan troglodytes* species on the grounds of manifestation of the neotenic features. Until recently, *Pan paniscus* was confused with the *Pan troglodytes* species or, at the most, was considered to be its subspecies. It was only the present-day science which contributed to the general knowledge of this rare species and elucidated its relation to the next species of *Pan troglodytes* and other primates (Goodman et al. 1970, Cronin 1975, 1977, Khudr et al. 1973, Cramer 1977). A clear differentiation between these species can be based already on the proper length of the mandibula (Cramer 1977). The sexual dimorphism of the *Pan paniscus* species is evident only in a canine tooth and body weight, but not in the whole dentition, cranial capacity, facial features, length of long bones or their robustness (Cramer and Zihlman 1976). Zihlman and Cramer (1978) performed a morphological analysis of 21 skeletons of the *Pan paniscus* species and found some significant difference between clavicles, shoulder-blades, pelvises, the humerus: femur length ratios and lengths of femur and humerus heads. Considering the fact that both species exhibit an extensive overlapping of body weights the observed differences cannot be explained just by the body size. It is possible and perhaps probable that the above features are those which evolved during the phylogenesis of the *Pan paniscus* species from the features of a common ancestor of this species and the *Pan troglodytes* species by means of neoteny. However, the present state of research does not permit us to identify this ancestor in order to verify this presumption. Besides that there is a possibility that this hypothetical ancestor simply did not exist and that *Pan paniscus*

species evolved by means of neoteny directly from *Pan troglodytes*. Yet, no matter what development actually took place it is important that both of these species yield a very reliable support of the idea of involvement of neoteny as a phylogenetic mechanisms in the evolution of primates.

A significant evidence of neoteny in the evolution of man is the obvious reduction of splanchnocranium with respect to neurocranium. At the same time we need not proceed from the comparison with the modern apes as we have at our disposal some more or less preserved hominid neurocrania and jaws (maxillae and mandibulae). Besides that, if we compare the fetus of the modern man with the adult individuals and with the fossil adult forms we find that, as far as the relation between splanchnocranium and neurocranium is concerned, the fetus resembles more the adult modern man than the adult ancestors. This fact is in no case in contradiction with the theories explaining the reduction of splanchnocranium by the change in distribution of stresses on the masticating apparatus resulting, e.g., from nutritional changes or changes in the mode of locomotion. On the contrary, this fact complements these theories as only in this way it permits us to understand the biological mechanism which served as a basis for the mentioned reduction of splanchnocranium (this understanding is naturally possible only in the closest connection with other factors linked with, and exerting influence upon, this mechanism).

NEOTENY AND THE EVOLUTION OF HUMAN BRAIN

In the phylogenetic development of man neoteny played a part essentially in the evolution of human brain. If we consider neoteny on the basis of individual ontogenetic heterochronies of the progressive retardation type (i.e. on the grounds of neoteny proper ontogenetic neoteny) as a phylogenetic mechanism, we are offered an opportunity to understand and explain the way which led during the evolution of man to an acquisition of a relatively big and efficient brain. This process occurred in two ways: directly and indirectly.

In the first case an allometric change of size of individual structures (i.e. internal changes in the structure of hominid brain) took place. We observe, e.g., a very conspicuous reduction of the olfactory lobes (this reduction takes place naturally also in other apes), which reaches its maximum in man, an increase of the number of glia, and some other changes in the size of certain parts of brain; these changes must have necessarily affected the brain structure in general as well as its function. As far as glia are concerned, it seems probable that the more is the process of brain evolution accentuated and preferred, the higher is the increase in the number of glia. It is a known fact that human brain is approximately four times bigger than that of chimpanzee, yet it contains only 1.25 times more neurons (Shariff 1953, Holloway 1968). It is also evident

that the absolute size of neurons is in a positive correlation with the increase in brain size (Rensch 1959). Besides that we also presume that a bigger mammalian brain contains a more extensive dendrite branching as compared with that of a smaller brain (Holloway 1968, Jerison 1973). The highest concentration of glia occurs around axons and dendrites, and this tendency is the most marked in the cortex. According to Tower and Young (1973) the glia:neurons quotient represents in man fully one third of the total increase in brain size. The significance of changes in the mutual proportions in brain was demonstrated by the excellent studies of Holloway (1966, 1968, 1969, 1972), who came to the conception of a gradual "reorganization" of the brain structure during the course of evolution of man (Holloway 1976). Besides other ideas these studies show that identical volumes of brain in different primates need not be (and certainly are not) equivalent anatomically or functionally. The quality that matters is the degree of representation of the brain's evolutionally progressive structures. Nevertheless, the Holloway's "reorganization" of the brain in the phyletic succession of man was (as deduced from the brain structure of the present-day man) connected with (at least at a certain stage and up to a certain level of hominization, i.e. probably until the emergence of the *Homo erectus* form — the first undoubted man) a relative quantitative increase in brain size, i.e. with a growth of its volume as compared with the size of body (expressed by weight).

We come now to the second, indirect role of neoteny in the phylogenesis of human brain. The brain as a whole grows relatively during phylogenesis due to the fact that a number of other body structures juvenilizes, i.e., the ontogenetic retardation which projects itself into phylogenesis as a neoteny starts playing its role. It seems quite probable that the cause of phylogenetic relative growth of brain size as well as the cause for gracilization and, from the point of view of morphogenesis, premature termination of development of a number of other body structures and features is the very ontogenetic accentuation and preference of the morphogenetic evolution of the brain. Sacher and Staffeldt (1974) in their study came to a conclusion that from ontogenetic point of view the growth of brain size represents a process which imposes limitations on the growth rate of other elements of somatic growth (it represents a restricting factor for these elements). The authors furthermore claim that the cube root of the brain weight increases linearly with the time of gestation. This rule is then related not only to the ontogenesis of fetal brain within the framework of one species, but to the phylogenetic relation between the time of gestation and the neonatal weight (i.e. weight at birth) of the brain as well. We now come to an important conclusion that the time necessary for brain to reach certain level of morphogenetic development or to reach its full maturity may be estimated from the knowledge of its size as much. According to the ideas of the mentioned authors this finding represents an objective base for the estimation of relative maturation times of related species'

brains which differ in size. The authors also claim that this permits us to estimate the time of maturation or attainment of a certain size of brain of a fossil ancestor. Because the brain growth determines as well as restricts morphogenesis and growth of other tissues it is possible to deduce (on the grounds of brain proportions — or its size — of man and his fossil ancestor) also the morphogenetic state (or more precisely degree of maturity) of other structures. This knowledge provides us once again with a better base for discussions about the levels of ontogenetic development on which the individual compared structures take place (Sacher 1975). However, I believe that the estimation of morphogenetic state of individual body structures in the phylogenesis of man according to Sacher and Staffeldt should be done at least very cautiously. That is to say, the formation of the rule is achieved on the grounds of consideration about the ontogenesis of brain of a number of different species of mammals living in the most diverse environments and having passed through a very diversified evolution. Another very important objection could be raised against Sacher's presumption that the brain maturation takes place in the prenatal period, although it is a well known fact that the human brain keeps developing a long time after birth. The applicability of this rule to the estimation of morphogenetic state of individual structures in the phylogenetic process (and thus the consideration of neoteny in the phylogenetic succession of man by means of this rule) is also limited by the so-called neonatal brain growth advancement (as mentioned by Sacher himself), i.e. by a decrease in the size-of-brain-at-birth to size-of-brain-at-maturity proportion. In the modern pongids and terrestrial monkeys this factor is represented by values of 0.35 and 0.40 respectively, to which corresponds a weight of the big human brain at birth of 400–550 grams (approximately). As a rule, this weight is too high to ensure a successful delivery. We still know nothing about when had this weight reduction taken place. It is, however, positively connected with restrictions imposed by the delivery ways caused by the evolution of a new mode of locomotion in hominids — the bipedalism. If we, however, consider both the length of the morphogenetic process regardless of the time of gestation, and the effect of brain growth on the growth of other body structures (or at least some body structures — as discussed by Sacher and Staffeldt), we are offered an opportunity to consider neoteny of individual human features by means of determination of length of brain maturation in fossil ancestors.

Until the present time we have considered only the relative proportions, relative relations or relative sizes. It is, however, beyond any doubt that also the absolute growth increments and absolute increase in size of individual structures played part in human phylogenesis. In the case of evolution of the hominid brain it is quite probable that starting from *Homo erectus* a further brain-size increase is isometric, i.e., proportional to that of other structures and not leading to the relative increase in brain size (i.e. increase of the brain weight/body weight ratio — the so called cephalization coefficient). Accord-

ing to some students the relative brain growth terminated even earlier somewhere at the level of plio-pleistocene hominids (Tobias 1971, Holloway 1973, Lovejoy and Heiple 1970 etc.), in which we already encounter the survival of junctures till the late adult age, and other relative changes in size have to do only with individual parts of brain within the framework of isometric, absolute growth in size or volume of the brain. Only further research will show whether this is true as we still have difficulties with the appreciation of weight and size of the extinct forms.

If we use the allometric relation (i.e. relation between a part of the whole and a whole, itself, which, being a general and descriptive method, cannot on its own reveal biological and social causes of the processes leading to the generation of the brain of the present-day man, but which is valuable for illustration and description of quantitative changes of the monitored parameters) we actually come to the following possibilities:

- a) the ratio of brain volume to body weight (i.e. brain size to body size) does not change and the brain growth is proportional to the body-weight growth;
- b) this ratio changes and the weight (size) growth expressed by volume is relatively higher;
- c) ratio of the individual parts (i.e. their size) of the brain with regard to the brain as a whole does not change, the possible growth of individual parts of brain is proportional;
- d) the ratios of the individual parts of brain with regard to the brain size as a whole changes, some regions of brain relatively increase in size during the course of phylogenesis.

All these mentioned possibilities undoubtedly played some part during the course of the process of hominization (and not only in the evolution of man); this could have happened in different forms and in different stages of evolution and in different combinations. If we, however, reconstruct anthropogenesis from the viewpoint of brain evolution we find that the highest selective value at the beginning of hominization belonged to the tendency denoted as b) which gradually faded out and was replaced by the tendency summarized under c). These two tendencies, the basis of which is neoteny, did not ascend strictly successively (as it was already mentioned) but they intercalated into each other with one dominating first and the other later. Furthermore these two dependencies were combined with the isometric growth with regard to both the body and the brain as a whole [points a) and b)].

SIGNIFICANCE OF NEOTENY AND SOME HOMINIZATION FACTORS IN THE HOMINIZATION PROCESS

The process of hominization can be principally characterized by four basic factors:

1. attainment of the bipedal locomotion stage,

2. appearance of the hominid character brain and the hand-brain complex,
3. appearance of the material culture, and
4. development of hominid social organization and the human social level.

The first two factors are of a biological character and are phylogenetically the older ones. We presume (Vančata and Přivratský in press) that neoteny played a role in some forms even before the advent of the hominid succession. A very significant moment during the course of hominid evolution is the liberation of fore limbs from the locomotor function. The hind (or lower) limbs become the exclusive organ of locomotion and the part of brain capacity originally burdened with controlling the locomotor function of the fore limbs becomes free. Therefore a capacity for introducing other, new functions appeared without forcing the brain to increase in size. In a gradual development this original capacity was really exploited up to its upper limit for a creative activity of the upper limbs (the appearance of the hand-brain complex). In those forms in which neoteny still played a role (in the brain evolution also indirectly) this limit was during the hominization process unceasingly shifted and biological compensation of the ever increasing demands on the higher nerve activity took place. The forms in which neoteny (especially of the brain) manifested itself in a limited extent only (or not at all) remain on a subhuman stage of development, though they used maximally the given possibilities of the brain, whose size thus became the decisive factor. In this situation the increase in brain size represented a considerable selective value. This, however, represents a precondition for both the further improvement of the hand activity and the regressive effect of this activity on the versatile development of brain.

The hominid brain thus kept, during the course of hominization, growing in size until it reached in the late erectoid forms the size comparable with the brain volume of the sapient man. This tendency was accompanied by a stronger trend of a more intensive utilization of brain activities reflecting the needs of a developing human society. The tool in this process of intensification became the new, communicative character i.e. language. Hand in hand with the gradual appearance of a human social level of behaviour there appeared the quality of speech — its combinatorial character. It seems probable that the predecessors of man used a gesture language, i.e. a symbolic language which rendered possible only a limited, minimal combinatorics. The gestures were, however, gradually replaced with sounds; sound language was more suitable for the necessary and very important communication in coordination of hunt that was taking place, e.g., in forest or in twilight etc. The combinatorial character of language appears when various combinations of a certain and limited number of sounds form signs. The number of these basic sounds is relatively small (roughly 30 to 40), yet the possibility of their combination is practically limitless. The "extensive" utilization of

brain matter of man's predecessors connected with a relative and absolute growth of brain and rendered possible by the gradual neotenzionization of the human phyletic line is gradually replaced by an "intensive" utilization of the brain. The symbolic, but noncombinatorial, language was in this way gradually replaced by a symbolic language allowing combinations. It was just this combinatorial character of language that opened up practically unlimited informative possibilities. In general there must have existed biological preconditions of the appearance of this language. Let us have a brief look at several allometric changes in proportions of individual brain structures which took place in phylogenesis on the basis of neoteny together with the increase in brain size.

It is not the frontal lobe of the brain cortex which underwent the biggest changes during the process of hominization though this hypothesis was proposed in a majority of older studies. In comparing the frontal parts of the brain of australopithecines (the cranial casts have been compared) and the modern man we find only very minute differences in the size of the frontal lobe, while the parietal lobes considerable increased during the course of anthropogenesis. The increase in the relative height of cerebellum is also remarkable (Bonin 1963). Rather hypothetical is the presumption that during the evolution of human brain the grey matter in quantity grew, especially as to asteric neurons of the grey matter with short and branching exons, yet it remains a fact that in comparison with other primates man possesses more of these structures. From this point of view a strong reduction of direct outputs of structure of the extrapyramidal system took place during phylogenesis of man while the importance of nerve outputs through the cortex grew. The language, being a highly integrated function, attached itself by some manner (which has not been satisfactorily explained yet) to the region of first temporal gyrus. However, it seems that the detailed analysis of the lingual region of cortex will not yield much new information (Schuell 1960). For instance, the Broca centre (the promontory of the third left frontal convolution) retained merely a more or less historic significance. Besides that it is a long time since the cytoarchitectonic research proved that this is present also in apes and monkeys (Kreht 1936) in which the appropriate excitation of this region brings about similar movements of tongue and larynx as in speaking man. Remarkable is also the fact that surgical removal of the "speech centrum" (Pool 1949, Penfield 1959) did not in the least affect the lingual abilities of patients for several weeks. According to Bonin (1963) a higher significance from the lingual point of view has the temporal lobe, and especially the acoustic area, in which an integration of immediate memory and acoustic perception takes place. This integration is inevitable for the comprehension of spoken language as well as for the ability to pronounce not only one or two words, but the whole sentences. Already 20 years ago Chapman and Wolf showed (1959) that the highly integrated functions of the brain (to which the speech also belongs) are first of all damaged by an excessive de-

crease of brain matter quantity (especially the cortex) but not by the loss of brain tissue in some concrete region. It is therefore the quantity, not the localization, which plays a decisive role. Speech, the new quality in the process of hominization, is from the evolutionary point of view dependent on the development of a sufficient amount of appropriate nerve tissue and the quantitative development of certain regions of the brain cortex. The concrete expression of this condition in the process of hominization are the allometric changes in proportions, whose basis is neoteny. It is therefore evident that the combinatorial character of speech would not have been attained without the evolution of appropriate structures of brain and the brain as a whole. It is also evident that natural selection accentuated or preferred the evolution in this direction; in other words all the changes of the nervous system rendering possible the development of symbolic combinatorial speech were of a considerable selective value which follows from the way of social life. The brain, which man obtained as a heritage from his immediate predecessors, was actually the last organ that necessitated an "improvement". Although this "improvement" took place under the pressure of natural selection, the process of formation of a man has practically ended (Leonovitchová and Novák in press). The combinatorial system of speech and its cultural superstructures intensify the exploitation of the given brain capacity to such an extent that the further allometric changes in morphology, brain size and size of its structures cease being selectively significant and the selection to the advantage of a further intensification of neoteny terminates. Nevertheless neoteny reached in man maintains its level. The causes of its further existence are based on the phenomenon or factor which is, in turn, conditioned by neoteny. This factor is the last of the four mentioned factors of hominization (Vančata and Přivratský in press), i. e. the appearance and development of human social way of life. The consequence of the role of neoteny in the evolution of man is the expansion of brain connected with the relative immaturity of the offspring necessitating a relatively long maternal care. The infants are for a long time dependent on a group. On the one hand, this long-term dependence leads to a deepening and strengthening of the mutual social relations. The neotenic development of the brain renders possible a deeper and a longer process of learning as well as the appearance of other psychosocial properties.

In conclusion we may therefore say that neoteny, as a phylogenetic mechanism, made it possible to some forms to reach an evolutionary abbreviation during the process of hominization. As mentioned by Wierciński in his study (1978), neoteny was an energy-saving process, because it intensified and developed structures with a considerable selective value and thus accelerated the evolution of forms leading in phylogenesis to the contemporary man. Owing to neoteny and the tight linking of fundamental factors of hominization, man became an unequalled and the most successful organism of our planet's live nature.

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