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A CONTRIBUTION TO THE PROBLEM OF RELATIONSHIP BETWEEN SHAPE AND FUNCTION IN HUMAN EVOLUTION FROM THE POINT OF VIEW OF FUNCTIONAL ANALYSIS

ABSTRACT. — One of the basic aspects of the interpretation of the fossil material is the relationship of the function and the shape of the given part of skeleton. Antithetical character of data obtained from fossil and recent materials forces us to construct a hierarchical system in which the value of characters corresponds to a definite type of generality in the given structure. Features characterizing biological shape can have three sorts of character: either is their origin strictly genetically determined, or they are features without an unambiguous determination, occurring permanently owing to definite properties of the given structure (e.g., of the locomotor apparatus), and finally features, the quality and occurrence of which is not "strictly causal". As an example of a theoretical analysis that of features of femur and pelvis of hominids is given. Whereas in femur the three above levels of features can be in principle recognized, in pelvis, in view of the fact that it is a part of skeleton fulfilling both the locomotor and the reproductive function, the determination of features is much less unambiguous. Especially difficult is to delimitate the measure in which the expression of the studied feature is genetically determined. Solution of this problem will require a detailed elaboration of a whole series of ontogenetical and phylogenetical problems, both methodical and methodological ones.

The progress in the individual fields of the evolutionary anthropology provides solution to some problems. However, at the same time it gives rise to new questions. One of these new questions is the correspondence between the shape and the function; this question is connected with the problems of prediction of morphology of the soft body parts from the morphological shape of skeleton.

The only direct information could be obtained from the fossil material. Unfortunately, the offered information is distorted by time and its direct "deciphering" is impossible at present. The character of this information is vertical (phylogenetic), in contrast to that on the contemporary organisms which is horizontal (populationally-ontogenetic). Besides that, no categories (such as species and population), commonly used in the research on the recent orga-

nisms, can be used for the analysis of the hominid evolution (Wolpoff 1978, Pilbeam 1980). The definition of species, which is questionable even for the recent material, is inapplicable in the evolutionary research. The character of the population research on the recent hominids is completely different from that the fossil finds of individuals or their fragments. Also the methodology of obtaining information on the recent populations is inapplicable for the evolutionary analyses. For instance, the study of a one million-years long evolution of Plio-Pleistocene hominids in one locality would require an analysis of every single generation. With the average of 15 years for each generation the study would include 6 700 generations. In order to obtain at least a basic information we should study 10 individuals in each generation which means excavation of 67 000 indi-

viduals in one locality. If we presume the existence of three races or species, at least 100 localities should be investigated. Thus we come to the number of 6 700 000 individuals for the period of one million years. Such a presumption is absurd not only from the point of view of technical realization, but also because no such number of individuals has been preserved in one precisely defined stratigraphical position.

Although the fossil material does not provide abundance of data on one population, it offers us a unique information on the direction, rate and proportionality of evolution, and on the evolutionary trends (Wolpoff 1978, Day 1979). This material hidden in the fossil material. Findings on the recent material are of a quantitatively different character and cannot simply substitute those on the fossil one. These findings may be used in a concrete situation and for a concrete degree of abstraction as a sort of a "model aid" which helps to outline and construct picture of the past. Besides this, the findings on the recent material may be used for obtaining information of a general character, such as the heredity of shape, changes of the shape during ontogenesis and the functionality of the shape in the given type of conditions. In the case of the fossil material, the information of this type is fragmentary and very rare.

The question of biological shape and its functionality is therefore a very complicated fundamental question of the evolutionary anthropology. A new biological shape is a result of the active ontogenetic forming of the genetically determined basic shape. We know nothing about the mechanisms by which basic shapes become genetically fixed during phylogenesis, and by which external environmental factors (e.g. load, torque forces) win through during ontogenesis. We do not know as well which role natural selection has when certain basic shapes originate.

The term of active forming includes three groups of factors:

1. The directly and indirectly genetically controlled growth by internal regulatory mechanisms;
2. The environmental effects of short duration; and
3. The environmental effects of long duration.

The factors usually complement and condition each other, thus making the analysis of a certain shape a very complicated task. The functional factor is difficult to analyze and compare regressively with the shape even after separating it from other factors. The functional factor represents a compound and shielded vector which forces the functional (direct or indirect) response of the shape. However, the existence of such vectors is in many cases questionable. Certain shape possessing no selective advantages may appear in connection with the origin and existence of a qualitatively new shape. The shape may then preserve or even increase its expressivity even though the real functional use of it may appear later. Certain shape usually accomplishes several functions. Because none of the biological shapes is perfectly plastically variable the accom-

plishment of the functions is never perfect. This means that it is more advantageous to preserve a stable shape accomplishing several functions than a shape perfectly accomplishing only one function and not accomplishing other ones.

A shape should be therefore analyzed in context with shapes of the same structural level as well as with other ones. In the case of paleoanthropology we should compare the shape of a certain bone with shapes of other parts of skeleton, which represent components of the same functional unit (in all structural levels), and take into consideration those features of the skeleton, which point at a function of other structures (e.g. imprints of tendons, beginnings of muscles and ligaments).

Thus we approached the problem of correspondence between the soft and the bony parts of the skeleton. The problem can be easily solved if there exists a direct functional correspondence between the soft structure and the skeleton. If such a correspondence does not exist then we must try to find features that left imprints on the skeleton and that are closely correlated with the appropriate soft body parts.

Let us test now this notion of ours on some concrete examples.

In the first example we shall analyze the proximal part of femur of the Plio-Pleistocene hominids. This unit is relatively complex despite the fact that it accomplishes only one function — the locomotor one. We may differentiate between three groups of morphological characteristics.

The first group includes features of the hereditary character: a long antero-posteriorly flattened neck, a relatively small head (Zihlman 1970, Robinson 1972, McHenry and Corruccini 1976, 1978, Wood 1978), which is probably satisfactory for its function, i.e. efficient bipedal locomotion (Lovejoy 1975, 1976, 1978, Lovejoy et al. 1973, Vančata in press b), antero posteriorly flattened proximal part of diaphysis, relatively medial position of lesser trochanter and different shape (relatively lesser lateral flare) of greater trochanter (Napier 1965, Day 1969, 1978, Walker 1973, Thompkins 1977). The character of hereditary features, connected with the basic function (i.e. with locomotion), and the structure of the features is connected with the modification of the basic function (in this case with the bipedal locomotion). The character of the permanent hereditary features indicates only a general structure of the soft parts. However, a general frame for further investigations is satisfactory.

The second group consists of permanent non-hereditary features formed on the basis of interaction between the structure and the function. A typical example are the features connected with the formation of ligamentum iliofemorale and the hyperextension in the hip joint, i.e. properties characteristic for the efficient bipedality (Day, 1969, 1973, 1976, 1978, Thompkins 1977, Lovejoy 1975, 1976, Vančata in press b, c). The features include tuberculum femorale, linea intertrochanterica, linea spiralis (ligamentum iliofemorale), s. m. obturatorii

externi and s. m. psoatis (hyperextension in the hip joint). The complex of these features allows us to outline the structure of muscles and ligaments of a given region.

The last group is composed of features of an ontogenetical character. These features have no direct connection with the function the manifestation of which is variable. A typical feature may help to outline the morphological characteristics of the body soft parts. For instance, no cause of variability is known in the case of the collo-diaphysal angle. On the other hand, tuberositas glutea exhibits a typical development of gluteus maximus (although the same development could be expected also with the very poor manifestation of the given feature, as shown in the case of femurs of *Homo sapiens* — unpublished data — Vančata). We should not limit the study of features to that of only one functional group. On the contrary, we should analyze the whole functional group and the interconnected groups. In our case we deal with features of pelvis (which are directly connected with the femur — i.e. features typical of the biomechanical femoropelvic complex — and which morphologically characterize the whole pelvis) and other bones and joints (i.e. bony elements of the lower limb).

As a second example may serve the pelvis of the Plio-Pleistocene hominids. This case is more complicated because the pelvis accomplishes several qualitatively different functions. First, it accomplishes the locomotory function. The pelvis provides attachments for limbs and back and abdominal muscles. Second, it transfers the body weight to the lower limbs and absorbs shocks of the motion. Third, it provides protection for the internal organs. However, this statement is imprecise because the pelvis forms a support for structures which protect the internal organs. Fourth, the pelvis functions as a delivery channel.

Let us analyze now several features of pelvis of the Plio-Pleistocene hominids in connection with the mentioned functions.

In the case of the locomotor function we may find a number of morphological features of the hereditary character. The shape of ilium and especially iliac blades provides attachments for the gluteal muscles. As compared with the contemporary man they are broad, ventrally twisted and assume a more laterally oblique position. It is also the reinforcement of ilium for the attachment of the gluteal muscles, called iliac pillar, which assumes the anterior position in Australopithecines. Spina iliaca anterior superior, to which the oblique abdominal muscles ligamentum inguinale and musculus sartorius are attached, are, in comparison with man, positioned ventrally. Spina iliaca anterior inferior for the attachment of tendons of ligamentum iliofemorale and musculus rectus femoris is well developed. Sacrum is broadened in connection with the more lateral position of the gluteal muscles, which are the abductors of the bipedal locomotion (Zuckermann et al. 1973, Lovejoy 1976, 1978, Zihlman 1978).

In analyzing the bipedal locomotion of the fos-

sil hominids we usually compare the shape of their pelvis with that of the recent man. Due to the lateral position of the iliac blades and of other features different from those of the recent man some authors doubt the effective locomotion in these forms (Oxnard 1975, Zuckerman et al. 1973).

However, some recent biomechanical studies (Lovejoy 1976, 1978 and Zihlman 1978) show that the used procedure is not correct and that a slightly different may also accomplish the same function. For instance, the more anterior position of iliac pillar and the ventral elongation of spina anterior superior at the more lateral position of the hip blades renders possible insertion of muscles (similarly to that in the recent man) necessary for the bipedal locomotion. The difference between the type of walk of the Plio-Pleistocene hominids and the recent man is still being discussed.

It is difficult to differentiate between the hereditary features and permanently nonhereditary features conditioned by the function in the ontogenetic development. The basic shape is probably hereditary, though some characteristics of the apomorphic type could be permanently nonhereditary in both the Plio-Pleistocene hominids and the recent man. In the case of features of both types we may presume a great variability in the population and in the phylogenetic development.

Questionable is also the size and shape of ischium which was considered as "ape-like". This notion is dismissed as erroneous today. The analyses of the contemporary pelvis indicate that the shape of tubera ischiadica and the muscle impressions of "hamstrings" and of musculus abductor magnus are very variable, despite the fact that these muscles were fully functional in the mentioned individuals.

The achievement of the upright posture and of the bipedal locomotion changed the static demands made on pelvis (with respect to other higher primates). The characteristic feature connected with this function of the weight transfer are as follows: the typical increased area of the sacro-iliac joint (i.e. greater area of facies auriculares), formation of promontorium, a decreased distance between the hip and the sacro-iliac joints (Leutenegger 1977), and formation of a deep incisura ischiadica.

Changes of the pelvic shape as a consequence of the bipedal locomotion induced also changes in the birth channel shape. The pelvic inlet, limited by linea terminalis, is formed from the back by sacrum, from the sides by the iliac and pubic bones, and from the front by the pubic bones. The pelvis became broader, the transversal diameter of the pelvic inlet increased, while the sagittal diameter decreased. According to Leutenegger (1972) the parameters of the Sts-14 pelvis are 99.0 mm and 85.0 mm. The ratio of the transversal to the sagittal diameters is, in comparison with the contemporary man, even bigger. In the pelvic outlet the sagittal diameter is bigger than the transversal one. From the front it is limited by the lower part of symphysis, from the sides by the lower part of ischial bones and from the back by coccyx which makes the pelvic exit

smaller than that in apes. The heredity of features determining the shape and size of the pelvis minor is inevitable for the preservation of stable conditions during delivery. The mentioned features represent probably adaptations to bipedal locomotion. Because the head of the fetus of the Plio-Pleistocene hominids was probably small, the reproductive function did not play a significant role in the forming of pelvis at this stage of the process of hominization (Jordaan 1976).

With the increase of the cranial capacity during the development towards man the pelvis was reshaped, the hip blades achieved a more upright position and the delivery channel broadened (Lovejoy 1976). According to many researchers this stage was connected with the improvement of the bipedal locomotion.

According to Lovejoy (1975, 1978) the locomotion of the recent man is less advantageous from the biomechanical point of view. This opinion, however, does not come to the point because the pelvis of Australopithecines was adjusted to their type of locomotion which differed from that of ours. On the other hand, to say that pelvis of the Plio-Pleistocene hominids was unique is only mentioning of a well known fact.

When evaluating the correctness of our considerations according to the given examples it follows that they can be correct from a general point of view. However, these concrete examples also point at the methodological shortcomings of the contemporary functional morphology. No objective criteria for the appraisal of the shape exist and therefore the obtained information is difficult to interpret objectively. The contemporary morphometrical methods (both the multivariate analyses and the methods of shape transformations), which render possible an objective appraisal of the shape, cannot describe most features of the second and the third factor groups. This decreases their objectivity.

The difficult problems of relations between the shape and function can be solved. This will necessitate a cooperation between many specialists from different fields of science.

In the conclusion we would like to stress that the intention of this study was to attract attention to some problems, not to solve them. The study expresses our opinion on the possibilities and paths of investigation which may not be correct. However, this does not mean that the existing problems of the evolutionary anthropology do not have to be solved.

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