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UTILIZATION OF MATHEMATICAL METHODS IN THE STUDY OF THE HUMAN EVOLUTION: THE PROBLEM OF THE MORPHOFUNCTIONAL RESEARCH IN PALEOANTHROPOLOGY

ABSTRACT. — The endeavour to make morphological information objective resulted in introduction of mathematical and statistical methods in morphology. These methods are especially important when fossil material and the evolutionary process is investigated. The description of the biological shape is of utmost importance in the analysis of the fossil material. Parameters, characterizing the form have to be not only optimal, but also adequate to the problem in question. In biomechanical analyses mathematical modelling is of great importance, even if its methods have to be further developed, so that they would be consistent with given types of biological problems or would not simplify the problems too much. To evaluate results statistical methods are especially important, particularly when data are processed. It is necessary to consider thoroughly the suitability of the application of univariate or multivariate methods, both with the respect to the given problem and the potential results. Multivariate methods offer, in spite of their intricacy, results of complex character, which can be very useful especially in evolutionary studies. In the study the analysis of the proximal epiphysis of the femur of primates is used as a concrete example for the utilization of the multivariate methods. Transformations of the input data used show the possibilities of corrections when samples are deficient in various ways. Results of the treatment of groups with different systematical structure stress the necessity of a preliminary biological and evolutionary analysis of the sample before the proper application of the multivariate methods. Neglect of these principles could result in distorted or even erroneous results.

The only direct evidence about our biological predecessors are fossil remains of their skeletons, or, in some cases traces of their behavior. By this methodology of paleoanthropology and methods by which its research proceeds are given. The main object of the paleoanthropological research is thus the biological shape and its aim is to obtain the maximum information about the fossil shape and its function as well as to interpret the data obtained under conditions given by the degree of the knowledge concerning the corresponding period.

The oldest and still widely used methods enabling us to analyse the fossil material are the methods of the descriptive morphology. One of the greatest drawbacks of the classical descriptive morphology has been the small communicability as well as a subjectivity of the results obtained (a more detailed discussion of the problems of the descriptive morphology can be found elsewhere — see Vančata and Lukoveová, 1980, Vančata 1989a). For this reason attempts to reach a clean-cut quantification and thus an objectification of the results appeared already at the beginning of the present century (Pearson, Martin, Thompson, Fischer and many others).

Connection of quantitative biological methods with mathematical and physical methods resulted in a whole series of new branches of science (biocybernetics, biomechanics, morphometry and others). Thus also a branch of enormous importance for the contemporary paleoanthropology originated — morphometry, which became a basis of further branches important for paleoanthropology, e.g., of biomechanics. In view of the fact that biological processes and thus also biological features possess a stochastic
character. It is essential that corresponding mathematical theorems are used when considering these problems. In this way, the assistance of statistical and other methods becomes a logical extension of classical study of morphology and structural biology as well as paleontological disciplines.

6. It is not the aim of the present contribution to discuss the limitations of biometrical methods, but rather the possibilities and strategy of their application. Any restriction of the morphological data in a way that their absolute value can be used in subsequent analyses is justified as it reduces the complexity and serves to separate the different materials. Therefore, the results of a previous analysis of acoustic wave analysis, the classification of the material, and the comparison of the results of the different analyses are presented.

Mathematical Modelling

Mathematical modelling is a widely used tool in studies of biochemistry and also in studies of ontogenic growth or in reconstructions of the morphological evolution in phylogenetic trees.

Mathematical models are used in biochemical analyses to solve three basic problems, which, however, overlap in practice considerably:

1. Modelling of biochemical processes and phenomena.
2. Reconstruction of biochemical relationships in various parts of the skeleton of recent primates and their exploitation for interpretation of the evolution of the primates.
3. Clades of recent primate species, shape, and their exploitation for interpretation of the evolution of the primates.

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models have to be formed, which can be adapted to the presumed state of the pleco-genetically given studied form. Some recent attempts to produce such models (Yamazaki et al., 1975, Breuerhoff 1979) gave very interesting and useful results and have shown promising prospects of this approach. Studies aiming at modelling of the ontogenetic and phylogenetic processes solve given problems with the assistance of methods of shape transformations, based on Cartesian (Thompson 1961) or birethogonal transformations (Bookstein 1977, 1979). The most suitable for the description of growth processes appears to be the method of transformations of birethogonal grids developed by Bookstein (1977), which consistently starts from the characteristics proper to the given shape and is relatively simple but at the same time sufficiently exact and robust and hence also capable to bring about a correct and objective concerning the shape studied. However, the method is still in an initial stage of its development, for the time being it works with planar models and it is not yet quite clear how the spatial modelling will be carried out in practice. It may be that solution of this problem will be made possible by combination of the method of transformations of birethogonal grids with another method, capable of a description of shape in space (e.g. Oxnard 1973, Jooeklooghen 1980). Be this as it may, as soon as this method will be capable of practical application it can find a wide use in solving problems of the human evolution.

When studying morphological changes in the evolution of higher primates (hominoids) Cartesian transformations were predominantly used (e.g. Kummer 1952, Sarath 1967, Appleby and Jones 1976). The aim of these studies has been rather to illustrate the application of the shape transformations and not to carry out a real analysis of the morphological evolution of hominoids. Thus we can say that from an objective viewpoint the shape transformations have not yet found a wide application in evolutionary studies.

The results of modelling biological “problems” and application of these methods to the fossil material are the data of stochastic character. To process such data statistical methods may be used.

**Statistical Methods**

Since fossil data possess a specific character from the statistical point of view (low frequency samples are not homogenous, etc.) there are three possible approaches to process fossil data. Firstly, not to use statistical processing of the data at all, since statistical methods are either unsuitable or cannot give significant results. Secondly, the data can be processed using methods modified for the solution of the given problem. Thirdly, the data can be processed by statistical methods without fundamental adaptations (even if some modifications can be useful). At this point either the input data are transformed or output data are modified according to specific characteristic or the method in question.

The first possibility is, of course, no solution at all, the second method is applicable only in simple univariate or bivariate methods and only the third method is a real and universal one, especially in more complex univariate and multivariate methods.

It has to be noted that the modification of the output data can be on the one hand very elegant, efficient and precise, however, that on the other the risk of a possible desinterpretation of the data is in most cases too high (e.g. Oxnard 1973, 1975, 1979a, b). This is the reason for the time being appears to be the transformation of the input data (Vanata and Lazánková 1980).

Since most modern statistical methods start from the postulate of normal or at least quasinormal distribution of the data in the studied sample (e.g. Blackith and Reymont 1971, Oxnard 1973, Maxwell 1972, etc.), it is necessary to carry out transformations which, apart of special requirements, also “normalize” the parameterization of parameters in the sample. Such transformations can be e.g., logarithmic transformations and various standardizations and corrections (e.g., concerning the size or allometry) of the input data. In any case be this type of transformations carried out by indexes, which, it is true, remove the effect of size when two shapes are compared (and even remove it absolutely), but which have no “normalizing” effect.

For the processing of the data itself either methods working with individual variables (i.e. univariate and bivariate methods), or methods working with the complex of data (i.e. multivariate methods) can be used.

Univariate methods give a valuable primary information and characteristics of the sample. This information may be of a considerable assistance to obtain orientation in the problems and also decision about the further proceedings (e.g., the use of standardizations and ratio-diagram, correlation and regression).

The usefulness and vividness of the use of the ratio-diagram can be illustrated on the analysis of the proximal femur of hominoids, characterized by four fourteen variables. When a series of standardized variables is compared a single morphological trend in Plio-Pleistocene hominoids is clearly apparent, opposite to in many aspects to the trend of the oldest sapient forms and obviously to a certain degree also to the trend in Homo erectus (Fig. 1). Perceptible is also the morphological similarity of sapient forms, however, a greater robustness of Neanderthal man is obvious (Fig. 2). It is especially Pán and Pongo, in which similar metric characteristics can be observed, that differ from the recent man in the framework of hominoids. Conclusions derived on the basis of this very simple procedure were later confirmed by further more detailed analyses also on a more general level (Vanata 1980a, b).

**Multivariate Methods**

When the shape is studied as a whole the application of univariate methods is necessarily limited.
since they start from individual variables. Multivariate methods are more complicated, however, they take into account all variables. Let us therefore turn our attention directly to these methods.

Multivariate methods represent according to their approach to the processing of data three groups (more exact and complete information can be found elsewhere — Vanbuita 1980a, Vanbuita and Lukavec 1980). 1. Methods studying relations between individual groups (discriminant analyses, IP, P2 generalization of distance analyses and analyses of canonical variables), 2. methods studying all individuals as parts of a single sample, aiming at generation of new uncorrelated variables and, if need be, also of other characteristics of the sample (principal components analysis, principal coordinates analysis, factor analysis and, with certain reservations, the analysis of variation MANOVA, and multiple regression analysis) and 3. clustering methods, which on the basis of mathematical similarity cluster individuals into groups (hierarchic and non-hierarchic types of cluster analyses).

It is understandable that the picture given above is very simplified, however, it shows sufficiently clearly on which main principles are these methods based. With all analyses of the discrimination type it is necessary to have the criteria for each group studied determined already before the proper analysis. In some types of the discriminant analyses, however, it is not necessary to eliminate the disturbing influence of some variables (BMDP2M stepwise discriminant analysis — Dixon 1975, Van Vark 1976). Second group of analyses does not require an a priori knowledge of the characteristics of the sample with the exception of the basic data, however, it requires either homogeneity of the sample (when R-matrix starting from correlations between variables is used classically) or the knowledge of the specific composition of the sample and eventual elimination of the disturbing influence of some variables. If the sample is too non-homogeneous it is better to use the Q-mode, i.e. to start from correlations among individuals rather than among variables. Cluster methods require neither knowledge of the characteristics of the sample, nor a special adjustment of the data. They work on the basis of comparison of the coefficients of similarity of the individuals, hence they create groups (clusters) on the basis of the input data. Even if the method itself is independent of the inserted data, its results are very sensitive to the influence of the character of these data. For this reason the cluster analysis can serve to the forming of groups, but biologically real groups can be obtained only when biologically significant data are used.

Until now very many studies were dedicated to analyses and critical reviews of the general mathematical and statistical exactness of certain statistical methods (e.g. Kowalski 1972, Corracini 1975, 1978, Oxford 1972, 1975, Van Vark 1976). It has to be said that only very few studies considered the biological basis of the composition of samples and to a considerable degree the same applies to the biological character of the variables. However, mathematical is only an auxiliary method, which should assist the solution of biological problems. Thus the starting point for solution of the problem is determination of biological parameters of the sample and of requirements on the mathematical apparatus in view of solving a concrete biological problem, after which a choice of concrete mathematical methods should follow. For this reason let us terminate the present study by a practical example.

Using multivariate analyses from programs BMDP (Dixon 1975) two samples were studied: Hominidae (man, Neanderthal man, Plio-Pleistocene hominids; 88 females) and Homininae (Hominidae, gorillas, chimpanzees and orangutans; 117 females). Three types of analysis were used: cluster analysis BMDP2M, factor analysis BMDP4M and stepwise discriminant analysis BMDP7M. Apart of the "raw" data also four types of transformation of the input data were used: logarithmic transformation \( x \rightarrow \log(x) \), logarithmic standardization \( x \rightarrow \frac{\log(x)}{\log\log(x)} \), which had at the same time increased the "normality" of the distribution of the data in the sample.

**CLUSTER ANALYSIS**

Results of the cluster analysis in the sample Hominidae confirm the close morphological affinity of the individual groups of hominids (and to a considerable degree also of hominoids), Plio-Pleistocene hominids display characteristics, suggesting their mutual affinity; the femur ER 1481 approaches that of the recent man most closely. Results of the cluster analyses show that the results can change markedly already when the input data change little, e.g. when logarithmic transformation and standardization are used.

**FACTOR ANALYSIS**

Factor analysis results in three factors explaining in average 70% of the total variation (I. 30%, II. 21%, III. 19%). The first factor has character of size, the second and third are connected with deformations of the diaphysis, of the greater trochanter, and with dimensions of the neck (sequence and composition of individual factors is different analyses). The group of the Plio-Pleistocene hominids is with the exception of KNM ER 1481 different from the representatives of Homo sapiens (Figs. 3—5) and also from apes (Figs. 6—9). From apes gorilla is the closest to man, their mutual relations are difficult to define unambiguously.

If we compare the results of factor analyses between the groups of hominids (Figs. 2—5) and of hominoids (Figs. 6—9), then the results of factor scores (i.e. relations between individuals) are basically similar, however, the factor loading patterns are different. In the second and third factor the weren't variances, explained by these factors, differs considerably in the group of hominoids.
FIGURE 5. Principal components analysis for hominoid group (input data are logarithmically standardized).

FIGURE 6. Principal components analysis for hominoid group.

FIGURE 7. Principal components analysis for hominoid group (input data are logarithmically transformed).

FIGURE 8. Principal components analysis for hominoid group (input data are standardized).
DISCRIMINATION ANALYSIS

There are many analogies between the results of the discriminant analyses and those of factor analyses. The group of apes differs from that of hominids, gorillas being most closely related to man and certain relations between chimpanzee and orangutan can be found as well (Figs. 12—14). The group of Plio-Pleistocene hominids is homogeneous, only ER 1481 is classified with the probability 0.36 into the group of Homo sapiens (Figs. 10—11). Neanderthal man differs from the contemporary man and also, very markedly, from Plio-Pleistocene hominids by which the preliminary results of standardization (Figs. 1—2) are confirmed. In the individual discriminant functions occur most often: the width of the neck, head diameter, the biomechanical neck length and the distance from the base trochlear to the head. The average correctness of the classification into groups is 92.5%.

Results of all analyses of canonical variates are analogous (Figs. 10—14), however, appreciable differences can be found between the discriminant functions for hominids and hominoids.

If we compare the results of the cluster, factor and discriminant analyses in hominids and hominoids, for which there are two reasons. The first are easily and well interpretable from the biological point of view, since they express directly the morphological differences. Considerably more complicated is the interpretation of the analyses of hominoids, then the results of the analyses of hominoids reason is the considerable heterogeneity of characteristic patterns (i.e., morphological heterogeneity) for individual analyses (i.e., of factor loading patterns and discriminant functions), the second reason is the lower consistency of the sample, both morphological and phylogenetical. E.g., presence of some paralytic originating features (e.g., features resulting from the great body weight during the evolution of the skeletons of man and gorilla) can complicate the interpretation of the results considerably.
THE INFLUENCE OF THE SAMPLE STRUCTURE ON THE RESULTS OF Z. ANAS ASES

Let us close the above practical demonstration by the following consideration. If we carry out morphofunctional studies it is necessary to discriminate consistently, also as far as the hierarchy of the signification is concerned, between two types of the studied groups of individuals, differing in their basic structure. The former should contain phylogenetically related samples, which should be studied in order to observe the evolution of individual structures as a whole, whereas the latter should contain samples of different morphologies. In the second type of groups then should be studied behavioral evolution as a whole, it is necessary to search for analogies and parallels, which make it possible to interpret consistently problems in phylogenetically related groups. The establishment of the hierarchy is purely practical rather than theoretical, it results from the characteristic properties of multivariate methods. On the basis of results of these analyses groups of in general morphologically similar individuals are formed (as of individuals with similar parameters) and the differences and similarities between such individuals can be in many cases interpreted only with great difficulties without the knowledge of the morphofunctional differences in the corresponding phylogenetic groups. Multivariate techniques are composed of groups of satisfying optimizing criteria for the given method (e.g., that of the highest correlation or discrimination), regardless their object, and even individual features possess as results of the analysis itself, a biological meaning from the point of view of a problem to be solved. In other words, the objective result of the multivariate analysis need not have in this case any anachronistic value from the morphofunctional point of view, rather it points only to similarities or differences between different individual groups (structures) which can be exploited to further analyses, e.g., after the reduction of "noise" variables. I believe that neglect of these last and important reasons (structures) are the main reasons for contradictory opinions on the analyses of actually identical fossil samples.

CONCLUSION

In the present study I attempted to show the extent and possibilities of mathematical studies in research concerning the human evolution. Nowadays we can hardly imagine the investigation of the human evolution without these mathematical methods; their great significance is indisputable. The main problem rests, as it has been perhaps obvious from the above pages, in understanding and correct application of these methods. Mostly, however, the possibilities of mathematical methods as a unique source of quantitative information about the fossil material are not sufficiently used. It is often said that for a certain type of problems a definite type of analysis or modeling approach is suitable. This may be true to a certain extent but in no case does it mean that methods of different type cannot give important information, even if of a minor one. This fact becomes the more important, the more we realize how exceedingly significant is any information about the fossil material. For the complex of programs examining the problem from the most diverse viewpoints should be used in future, providing valuable information of complementary character. In this way the possibilities of investigation of fossil material would be considerably increased.

REFERENCES


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