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COMMENTS ON THE CONTEMPORARY SYSTEMA-TICS OF HOMINIDS

ABSTRACT. - Hominid systematics should respect not only the specific characters but also the general laws of systematics. The choice of the proper characters is one of the main problems. This characters must fit to the real evolution of the given group and not to respect pure classification of organisms only. Furthermore, the value of any selected character must be examined. This means for instance that the dentition need not be the best systematic identifier in all hominids because dentition has had changing selective value during hominid evolution. For this reason the dentition has been the source of many misinterpretations in hominid evolutionary studies. Several approaches to hominid systematics are examined. In insight to the problem between similary and interspecific relations is the second main problem of hominid systematics. Similarity is the primary source of the relations among populations, Three strategies of the transformation of similarity into type of relation (anagenetical, cladogenetical, and numerical taxonomical) are discused. The conclusion is proposed that functional evolutionary approach is inevitable for the consistent ho-minid systematics which should be based on the comparative studies of superfamily Hominoidea.

KEY WORDS: Homonid systematics — Methodology and general problems — Similarity and family relation

Systematics of hominids is one of the complicated and delicate problems of zoological systematics. These problems are due to two facts: firstly, systematics of hominids is laden with the methodological and systematic shortcomings of the contemporary systematics and, sencodly, hominids cannot be classified simply according to some general systematic pattern. Every systematic group is characterized by its own specific properties which should be taken into consideration similarly as the pre-requisites of the general sys-tematics. This holds also for hominids, which represent a unique group of organisms, and for which precise and detailed information is required (this information often exceeds the possibilities of the systematic analysis). However, no two types of systematics are admissible, one for hominids and one for the rest of organisms; this incorrect approach may be found in many anthropological studies. The general principles of evolution have to be applied to all organisms. The classification of organisms should have one common basis, otherwise the systematic groups will not be comparable and the classification will in general be meaningless. In the hominid group we deal with evolution of one family consisting of a small number of genera only. The situation is even more complicated in the Hominoidea superfamily due to a relatively short evolution (10-20 million years) and frequent radiations. These facts, together with the requirement of detailed results (man is that most intensively studied organism), make necessary numerous modifications of common zoological methods and call for a methodological and systematic precision and purity of the systematic methods. Anthropologists, as well as systematicists, should accept the factor of culture as a unique factor of the evolution of man. The generally accepted classification based on the concept of human races caused, due to an incorrect approach to the systematics of hominids, much confusion. It resulted in an overestimation of differences between human races, mirrored in numerous genera and species in the evolution of hominids (splitting), or in underlining the great variability of Homo sapiens mirrored in the lumping finds together into large units. Most zoologists favoured the lumping trend (e.g. Mayr 1950, 1963) and their opinion was accepted by most anthropologists. In their attempts to reconstruct the evolution of hominids and of other primates, and under the influence of zoological studies, some anthropologists and paleoprimatologists used models which were based on studies of recent primates (e.g. the study of sexual dimorphism in australopithecines poff, 1975, 1976a, b, c, d, 1978a, b; evolution of some hominid features — Jolly 1970). With the exeption of the functional studies the correctness of these analyses is questionable. The startling facts are the absence of functional analysis in systematic studies and failing to take into consideration the complexity of organisms and their existence in certain environment by most of the used classifications. The systematic classification was therefore based on the analysis of morphology and variability of those features, which were specialized (e.g. in teeth), and which were treated as equivalent; the functionally-systematic analysis was omitted. The classification features should not be accepted as constant factors which explicity classify an individual into certain group with respect to the fact that they have a different functional significance and different evolutionary value. In failing to accept this fact we may establish species and genera on the grounds of insignificant features despite the fact that these features are easily distinguishable; such species and genera will have nothing in common with the real evolution and will not be characterized by adaptations which were acquired by the organism and which played a significant role in its evolution (e.g. supraorbital arches and torus). The systematics should not turn into a pure science of classification, as it has often happened in anthropological studies. Systematics should be an analytical scienceyielding information on real evolution. A suitable type of analysis evokes an evolutionally-ecological approach to the systematics (cf. Mlíkovský 1983).

ystematics of hominids does not represent a simple identification of finds and their classification into certain taxonomic groups. Systematics is a scientific field which elucidates the phylogenesis of hominids. Systematic analysis determines the basic taxonomic groups, relations between these groups and their internal structure. Three basic fields of evolution are often misunderstood in the anthropological practice: phylogenesis (evolution of groups of organisms), evolution of features, and the systematic identification of an individual (cf. Mlíkovský 1983). For instance, evolution of dentition is often identified with the evolution of hominids or hominoids. Though dentition may be used as a good identifier, the chance of misinterpretation is high. This fact is documented by conpretation is high. This fact is documented by contradictory opinions of many specialists (Wolpoff 1975, 1976a, b, c, d, 1978; Robinson and Steudel 1973; Wallace 1975, 1978; Corruccini and Henderson 1978a, b; etc.). There are difficult problems with the introduction of hominid no-menclature. A basic shortcoming is the total absence of reliable and unambiguous definitions of hominid taxons. One taxon may thus be assigned to several phenons or, even worse, phenons may be assigned to non-existing taxons (because of their inprecise definition). Because of this si-

tuation every palaeo-anthropologist used the taxon in a manner suiting his purpose. Order can be brought into this field only by not accepting these inaccurately defined taxons. This measure, however, leads to an introduction of various working terms (e.g. robust and gracile australopithecines, advanced australopithecines, basal hominids) and results in a further confusion in nomenclature. Although the chief object of interest of palaeoanthropologists is the evolution of features and functional systems (e.g. locomotion, dentition, brain), the majority of anthropologists are well aware of the taxonomic continuum which is inconsistent with the traditionally set conception of systematics (cf. Mlíkovský 1983). This was one of the reasons due to which taxons were defined vaguely. Another reason was the absence of general criteria for the construction of taxon definitions. Thus appeared definitions of morphological (e.g. Tobias 1967), nutritional (Cachel 1975), ecological (Swendlung 1974) characters based on the authors' needs and were either incomplete or too general. The task of anthropological systematics is therefore to select a system of features which would sufficiently characterize the taxons of Hominids and which would meet the basic principles of general systematics (these principles should apply to all organisms including man). But even after the introduction of suitable definitions the selection of correct features, the most intricate problem remains unsolved. The fossil material, which may be used for the systematical analysis, can be studied only on the grounds of similarity, not of the family relationship (though the latter study would be more valuable). Unluckily, these two terms (similarity and family relationship) are often confused in the zoological, palaeontological and anthropological studies. In principle, similarity does not directly depend on phylogenesis and methods should therefore be invented to recognize the family relationship. The assertion that similarity does not directly depend on phylogenesis is not absolute. This assertion means that two related groups may, but need not, be similar, or that two groups may be similar and need not be related. This fact may be reflected in the relation between two groups in the following scheme:

two related groups may be similar because they are related and their new adaptations remain similar,

two related groups may be similar because their new adaptations are similar,

two related groups are not similar because their new adaptations were not similar,

- two related groups are not similar because they have

acquired new and different adaptations, two non-related groups are similar because their adapta-

tions were similar,

two non-related groups are similar because they have

acquired similar adaptations, two non-related groups are not similar because they have

acquired different adaptations, and

two non-related groups are not similar because they are not related and their new adaptations were not similar.

We may assert that two groups, which are related to a certain degree, are similar in some features to a certain degree. In principle this is correct but the relation between similarity and relationship holds for any level of generality. All representatives of the studied group of related organisms have a basic number of common and similar features and the more related the organisms are, the higher the number of these features is. However, these features are not substantial for the determinaton of family relationship in the group because they are common to all organisms in this group. The family relationship should therefore be analyzed according to other features and thus we once again return to the problem of similarity and family relationship. The family relationship in the palaeontological material cannot be found without evolutionary context (see Wiley 1981 for alternative view). The recent material offers substantially more possibilities for analyses of family relationship, but even here problems cannot be solved without analysing

phylogenesis of the group.

At present, three "strategies" of transformation of similarity into the criteria of family relationship are used in systematics. The original anthropological methods were based on classical taxonomic methods but the interpretation of their results has always been phylogenetical (even in the

ethnic anthropology). The definition of taxons has always been entirely intuitive, resulting in numerous differences in opinions (e.g. the different number of species and genera). Due to a consistent confrontation of opinions the fundaments of zoological methods later became more consistent and the classification became more precise; however. the inconsistence between concept of continuous evolution and the taxonomy, which is based on an unchanging and static concept of classification, cannot lead to a consequential solution of problems of the hominid systematics (the same holds for any other group of organisms). Problems of the hominid systematics were solved by some investigators in very unusual ways. For instance, Tobias (1969, 1973) proposed a bigeneric terminology, and Wolpoff (1971) and Brace et al. (1973) proposed a single species hypothesis. Some other hypotheses (geographic barrier hypothesis -Kortland 1972, 1974) tried to explain, within the framework of the old concept of taxonomy, the origin of these questionable taxons. These hypotheses as well as some classical anthropological hypotheses are based on an ana-genetical concept of phylogenesis. The shortcoming of this concept is the insufficient operative possibility at the appearance of new species and genera by radiation, while its merit is the consistent concept of time in the evolution. The most serious obstacle of the anagenetical concept is the fact that every group should be considered as o component of either the main (progressive) trend, or of the side trend.

Reaction to this mechanistic concept of evolution was the introduction of a cladogenetic concept of systematics which has been applied to anthropology as late in the seventies (e.g. Eldredge and Tattersall 1975, Delson 1978). Cladogenesis is based on finding couples of the phylogenetically most related groups and producing cladograms (cladistical trees) using these sister groups. As follows from deliberations on similarity and family relationship this type of analysis may also yield results which can be misinterpreted; such misinterpretation may occur when similarity and relationship are confused and when the time factor is neglected. Cladistic systematics imported to anthropology neither a new approach to the problems, nor any new hy-

potheses (c.f. Vančata 1986, but see Wiley 1981).

The third group is a numerical taxonomy. This taxonomy is actual a set of mathematical and statistical methods analysing similarity of several quantified parameters of an individual (these methods are usually denoted as multivariate analyses, though the methods most often used in numerical taxonomy are the so-called cluster analyses). These methods should be used both in anagenetical and the cladogenetical studies. It would be improper to present the results of analysis directly because there exist neither a computer, nor a computer program that should be able to transform the quality of similarity into the quality of family relationship correctly. In anthropology, and especially in the field of anthropogenesis, the methods of numerical taxonomy have not become common yet. A more detailed discussion of this topic is published elsewhere (Vančata and Lukavcová 1980, Vančata 1981, 1983, in press). On the other hand the used mathematical and statistical methods, forming the basis of the numerical taxonomy, are very unusual. They are used either for the classification purposes, e.g. the determination of race groups (Howells 1973, Corruccini 1978), and for the search of similarities and analogies between some features in fossil primates (Robinson and Steudel 1973, Bilsborough 1971, Corruccini and Ciochon 1978), or for functional purposes (Oxnard 1973, 1975; Corruccini et al. 1976, McHenry and Corruccini 1975, 1978; Feldsman 1976, etc.). This review shows that contemporary anthropology concentrates on a search for and on elaboration of methods, which could be used directly in systematics, and pays much less attention to the methodological problems of the systematics of hominids. Anthropology has thus achieved in many branches a high standard but the appropriate methods lack methodological reasoning. The methodological substance cannot be found only within the framework of one small group and systematics should not therefore be limited to the comprehension of problems only on this level. Systematics of hominids should be based on studies of the Hominoidea superfamily, and not of those of the Hominidae family. The reason for this is that the Hominidae family is not clearly defined and that the Hominoidea superfamily is more homogeneous from the systematical and evolutionary point of view (c.f. Mlíkovský 1983).

CONCLUSION

Besides the methodological and methodical principles we should adhere in the systematics of hominids to a certain degree of objectivity and correctness of the concrete studies. The results of analysis performed on a certain group in a system of organisms should neither be overestimated, nor underestimated (the same holds for every specialized field of systematic biology, including anthropology). This principle is usually confused with the necessity of specificity of analytical methods. The specific problem is the selection of suitable features for systematic analysis. The features are often selected according to their evolutionary significance. Features are therefore chosen without knowing their significance for the phylogenetical studies and their role in evolution. The found similarities need not be related with the substantial changes in phylogenesis of the given group of organisms. The selection of features depends on the experience and opinion of the investigator. Every research worker should therefore try to verify his theories in a broader context of evolutionary theories and to avoid thus mistakes and inaccuracies.

The intricacy of the evolution of organisms requires a complex analysis. Similarly, modern systematics requires a complex comprehension of the problem. In the systematics of hominids this means a broad and coordinated cooperation in many scientific fields (anthropology, archaeology, pa-laeontology, zoology, biochemistry, etc.), especially in the introduction of definitions of systematical units and in the selection of appropriate features for systematical analysis. The principles of general systematics should be always taken into account (cf. Mlíkovský 1983). This is the only possible way to the appreciation of phylogenesis of hominids and to the reconstruction and comprehension of evolution of significant hominid features.

ACKNOWLEDGEMENTS

I would like to express many thanks to Dr. Jiří Mlíkovský and Prof. V. J. A. Novák, for the thorough discussion of hominid systematics and taxonomy as well as general problems of systematics, which was extremely helpful for the elaboration of this paper.

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