Man and environment in the Palaeolithic
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Environment and human populations in Palaeolithic and post-Palaeolithic times: Two models of adaptation

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Abstract
Palaeolithic populations displayed a strong morphological differentiation. The average biological distance between groups from Europe is much more higher in the Palaeolithic than in subsequent periods. Palaeolithic populations differ from post-Palaeolithic ones on mortality structure, fertility structure, population size and density, biological state and dynamics etc., and also on response intensity to various environmental and cultural factors, i.e. the level of adaptability reactions (ecosensitive ones).
A great deal of anthropological papers showed biological consequences of "Neolithic revolution". Research objects were chiefly characteristics displaying a high level of reactions to ecological (environmental) factors such as nutrition, diseases, climate, soil composition etc. Individuals' responses to agents altering phenotypic formation of morphological traits were mainly analysed. Relatively few works concerned to the role of natural selection in morphological variability formation of Palaeolithic and post-Palaeolithic populations.
The paper deals with an estimation of opportunity for natural selection operating by differential mortality and differentiating fertility (differential reproduction) in Palaeolithic and post-Palaeolithic populations. On the ground of palaeodemographical and biodemographical data analysis of modern hunter-gatherers and agriculturalists' groups and morphological data it was shown, that in Palaeolithic differential death-rate (if occured: indirect evidence is an occurrence of a strong races origination process), particulary in the reproductive period, could be the main field of natural selection activity. In post-Palaeolithic populations severe decline of mortality is not observed, but rather intensification of this process in the first phase of neolithisation. At the same time processes of races origination are subject to diminution. Rapid increase of Neolithic populations density as in subsequent periods suggests considerable increase of fertility. We consider that just differential fertility and differential mortality in childhood could be the field of natural selection activity in these populations, but no differential mortality in reproductive period.
Adaptation of Palaeolithic populations was forced mostly by the system of the following factors: change of ecological zone or climatic alteration in occupied ecological zone caused (through differential mortality: fertility was relatively low, by the low variability of descendants' number) adaptive transformations of morphological structures. Distinctions between groups occupying different ecological zones were very strong and many morphological features had well-defined adaptive significance (mongoloid face, body proportions, steatophygia etc.).
Adaptation of post-Palaeolithic populations were forced mainly by the system of the following factors: ecological zone (intensively exploited, provided periodically plenty of food) was characterized by relatively stable ecological conditions, which inhibited need of strong morphological adaptation and abiotic and biotic environmental agents were partly buffered by the cultural system. Considerable increase of fertility became evident (on account of new ecological and living conditions), so as a great differentiation of descendents' number between individuals. Differential fertility afforded opportunity for natural selection, so for changes of adaptive nature. Different way of natural selection activity could be connected with other criteria of adaptation. Empirical evidence proves that in post-Palaeolithic populations individuals' ecosensitivity became an important criterion of adaptation. Great number and density of groups and a great fertility generated new relation in a system: environmental conditions - biological structure of a group.
It seems (on the ground of morphological differentiation of Neolithic and post-Neolithic groups research) that previously important adaptive morphological features "lost" their former adaptive significance considering new cultural equipment of groups. In these populations individuals' ecosensitivity and morphological structure, meeting new living conditions (nutritional stress, disease, developmental stress) became an essential adaptive criterion, so morphological processes of structural reduction (body size reduction, gracilisation, sexual dimorphism etc.) increased.

Key words: Palaeolithic and post-Palaeolithic human populations, natural selection, mortality, fertility, adaptation

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Introduction

The subject touched in the title of the paper is very extensive. The study of the relation between man and his environment has been conducted for many years by specialists in different branches of general anthropology. Because of that we will discuss in this paper problems, that are important for the aim of the research.

Numerous works were devoted to biological consequences of the transition from Palaeolithic to Neolithic and post-Neolithic economy, social structure and ideological systems. It was revealed, that this transition caused many essential changes in human skeletal structure and also in population characteristics, such as fertility structure, mortality structure, population size and density, mobility, mating system, diet, illnesses structure etc. (Ammerman 1975; Bennett 1976; Carneiro & Hilse 1966; Hassan 1981; Meiklejohn et al. 1984; Piontek 1989; Trinkaus 1983; Vallois 1960; Vampolova & Vančata 1993; Wierciński 1985).

Models created in order to explain the reasons of changes are usually of descriptive nature. They exhibit contributions of each biological or ecological component in the modification of individuals' or population biological features. In these models one describes the adaptation process, but does not inform exactly, if it is of genetic or only modification character (Larsen 1987).

Approach

Therefore two questions arise:
(a) Are the changes adaptive ones of genetic nature? (they cause alterations in the population genetic structure).
(b) Are the changes connected with adaptability or adjustment? - they do not cause alterations in genetic structure, but only constitute phenotypical individual response to environmental factors.

In physical anthropology there are controversies about the role of natural selection in changes of human populations. Attempts to describe an adaptive significance of different human morphological features are still incomplete (compare Bielicki 1975; Frayer 1981) and the models of operating of natural selection remain controversial.

Many physical anthropologists explain the biological consequences of transition to agriculture as changes in adaptability, caused by such factors as change in work demand on the body, as change in work demand on the masticatory apparatus, as change in food composition, as change in settlement pattern etc. (Carlson & Van Gerven 1973; Cohen & Armelagos 1984; Goodman et al. 1984; Huss-Ashmore et al. 1982). These are secondary and/or elementary factors, which are considered in multifactorial analysis as derivatives of the main factors. Multifactorial analysis requires an ecological approach. Such approach ensures also an analysis of the relations between main factors. No single factor operates in isolation and what is more important - the results of its impact in connection with other different factors can bring different effects (e.g. strong natural selection at small and large migration).

Factors forming the biological structure of human populations operate in the enviroment of cultural factors and in this connection their role and significance must be estimated from the point of view of general characteristic of the socio-cultural system. Such a characteristic can be explained by notion of an adaptive strategy. Adaptive strategy is understood as *"a pattern of adaptation, adaptability or/and adjustment to the environment in biological and/or cultural way "* (Wolański 1990, 4). This is the socially and culturally generated idea of relationship between man and his environment; therefore a class of fundamental cognitive assumptions is formulating human attitude towards perceived and analysed reality.

Adaptive strategy is generated in the human system, which can be determined as a class of elements (biological and cultural ones) ensuring the realization of human biological and cultural needs, and also system duration and reproduction. The human system is a class of elements and the adaptive strategy is a pattern of these elements arrangement.

In every human system at least five most important elements can be distinguished: biological one - human population, ecological one - human environment (abiotic, biotic, cultural), cultural ones, such as the economic structure, social structure, ideological control subsystem (Fig. 1).

The ideological control subsystem should be defined more precisely. According to Wierciński (1978) this is a social pattern of the world defining human status in it and the use of his doings. It contains the programs of social and economic

behaviour, that are prefered in some types of adaptive strategy. In other words, the ideological control subsystem, characteristic of hunters and gatherers, was completely different from the one characteristic of early agriculturalists. In hunting and gathering strategy the relations between the elements of the socio-cultural system were different from those in early agriculture or in subsequent periods. An attempt to compare the structure of the hunting-gathering system and early agriculture represents Fig. 2. Diagram A represents relations (main one and side ones) between the elements of hunting-gathering strategy (in Palaeolihic times), diagram B those in post-Palaeolithic systems (Fig. 2).

Ecological interpretation

In Palaeolithic times the relationship between the following elements was the most important relation: human population - human natural environment (abiotic and biotic) - economic structure. The social structure and ideological control subsystem were the factors, that ensured stability of the main relation.

In the transition to agriculture the relations between the main elements changed. Abiotic and biotic environment became the components of secondary importance. The relationships between human population, economic structure and social structure became the principal relation.

Table 1. General characteristics of the Palaeolithic and post-Palaeolithic types of adaptive strategy. (Pianka's model for r-selection and K-selection after Pianka 1970, 593 with modifications).

Factors	Palaeolithic populations	post-Palaeolithic populations
Climate	Fairly constant and/or predictable; more certain	Variable and/or unpredictable; uncertain
Mortality	More directed	Non-directed
Population size	Fairly constant in time, equilibrium; at or near carrying capacity	Variable in time, non-equilibrium; usually well below or above carrying capacity
Intragroups variability	Low	Medium to high
Intergroups variability	Strong	Medium to small
Opportunity for natural selection	By differential mortality	By differential fertility
Ecosensitivity	Low	High
Nutrition	Good quality protein	Poor quality protein
Leads to	Efficiency	Productivity
Selection favours	- Slower development - Delayed reproduction - Larger body size - Low maximal rate of increase	- Rapid development - Early reproduction - Small body size - High maximal rate of reproduction
Microevolution	Racogenesis and/or origin of local races	Secular trends in morphological traits

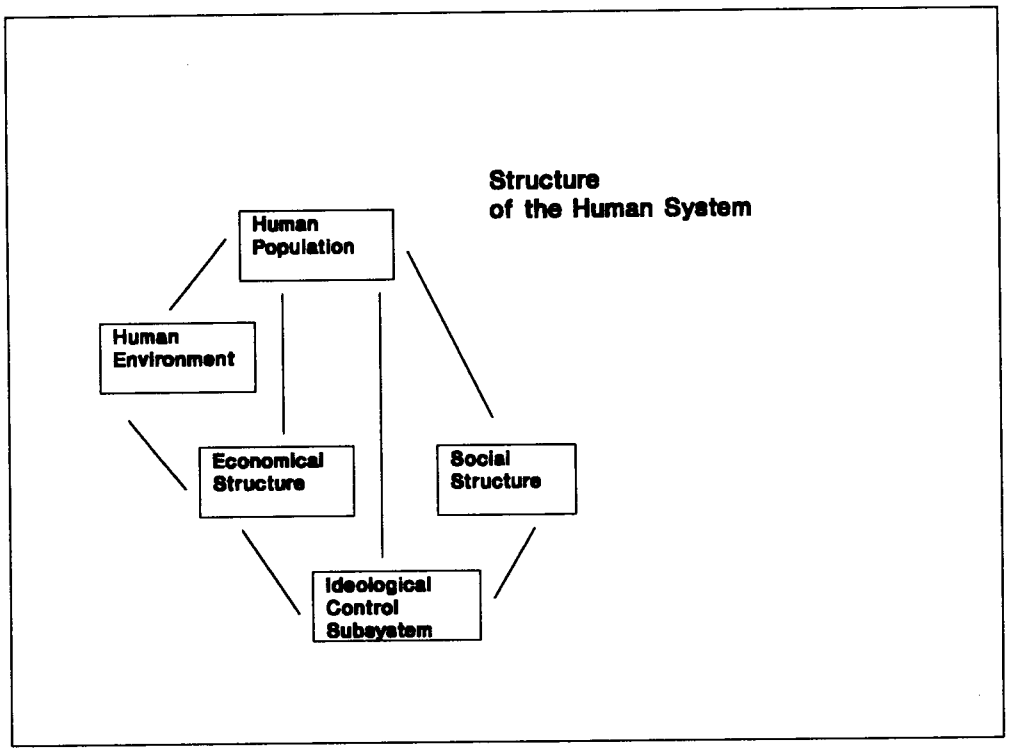

Fig. 1. The structure of the human system.

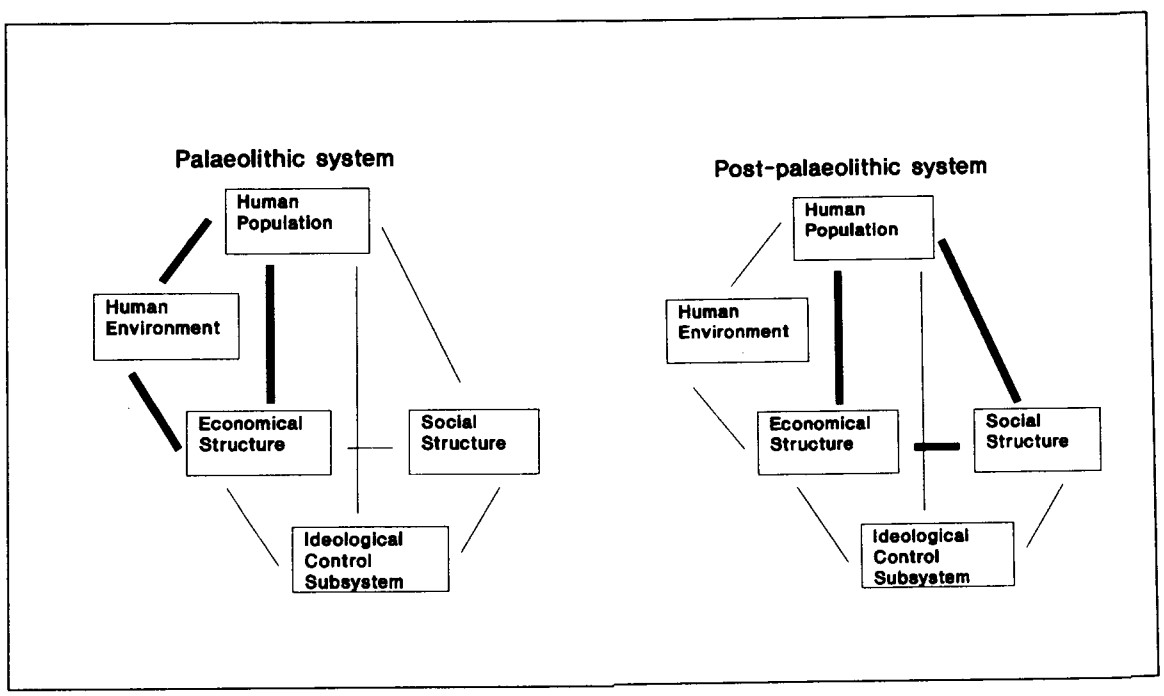

Fig. 2. The structure of the human system in the Palaeolithic and post-Palaeolithic type strategy of adaptation.

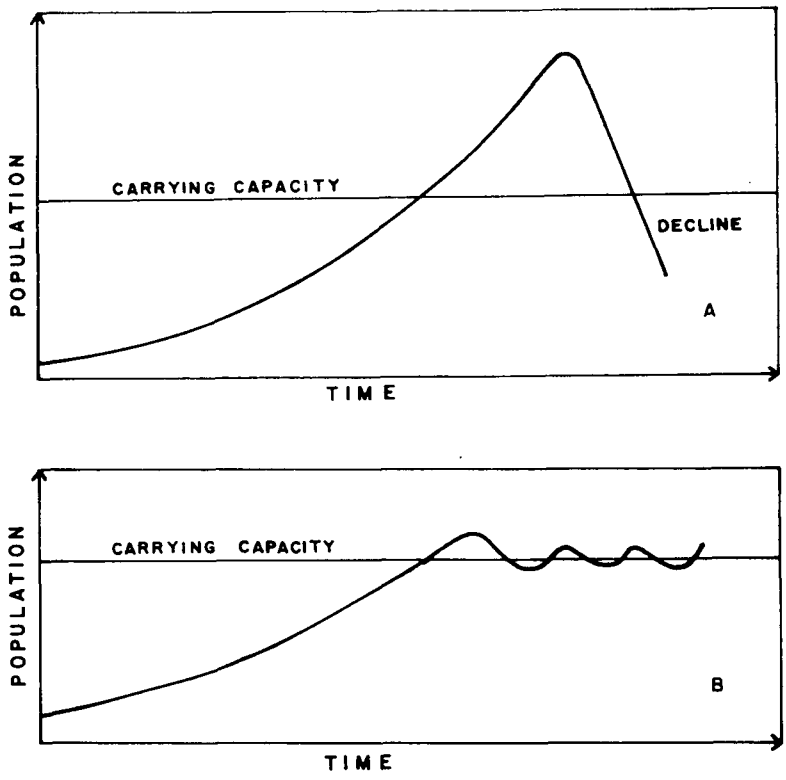

Fig. 3. Two types of population increase in relationships to carrying capacity (Hassan 1981).

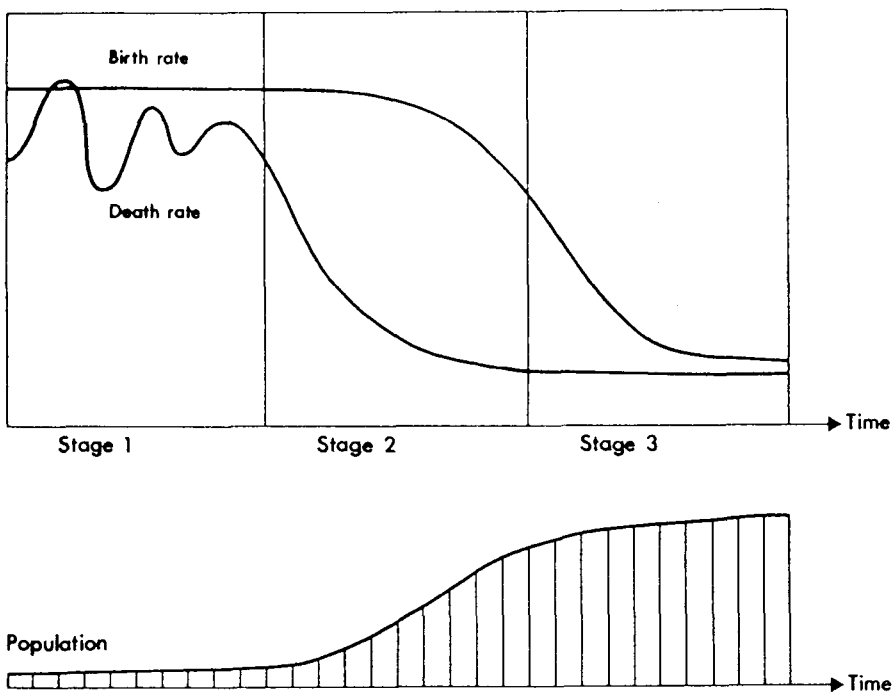

Fig. 4. The demographic cycle in the 19th century - model (Welinger 1979).

Relation change between the main elements in post-Palaeolithic populations carried the substantial ecological and biological consequences.

Palaeolithic populations displayed a characteristic pattern of population growth relative to carrying capacity (Model B), while post-Palaeolithic populations followed Model A (Fig. 3).

In post-Palaeolithic populations the abiotic and biotic environment stopped to be the most essential criterion of natural selection. As a result of cultural information these populations could also alter the level of carrying capacity with regard to typical of their economic structure. It caused an expansive type of population size growth, but also frequent economic and ecological crises, considering the extensive forms of natural environment exploitation (short-lived increase of carrying capacity caused environmental degradation).

In Palaeolithic populations biological adaptation was most important, which caused racogenesis; in post-Palaeolithic populations cultural adaptation became important, which caused ethnogenesis, migration, colonization, unification etc.

Biodemographical interpretation

The increase of population size and density in Neolithic times and in subsequent periods was like that in 19th century after the industrial revolution (Fig. 4). In 19th century a demographic revolution was caused by increase of population size with regard to strong mortality decline (in a reproductive and pre-reproductive period).

Similar pattern for transition to agriculture is assumed by other investigators, but comparisons of mortality structure of individuals in the reproductive period prove, that adults' mortality was higher in Neolithic than in Palaeolithic populations (Fig. 5). Similar results were described by Wittwer-Backofen (1989). Ammerman (1989, 68) noticed, that *"in pre-industrial England fertility is more responsive to changing economic conditions than mortality. The normal for demographic archaeology, with its natural inclination towards mortality (since it alone can be measured from skeletal data), is that fertility warrants far greater attention than it normally receives".*

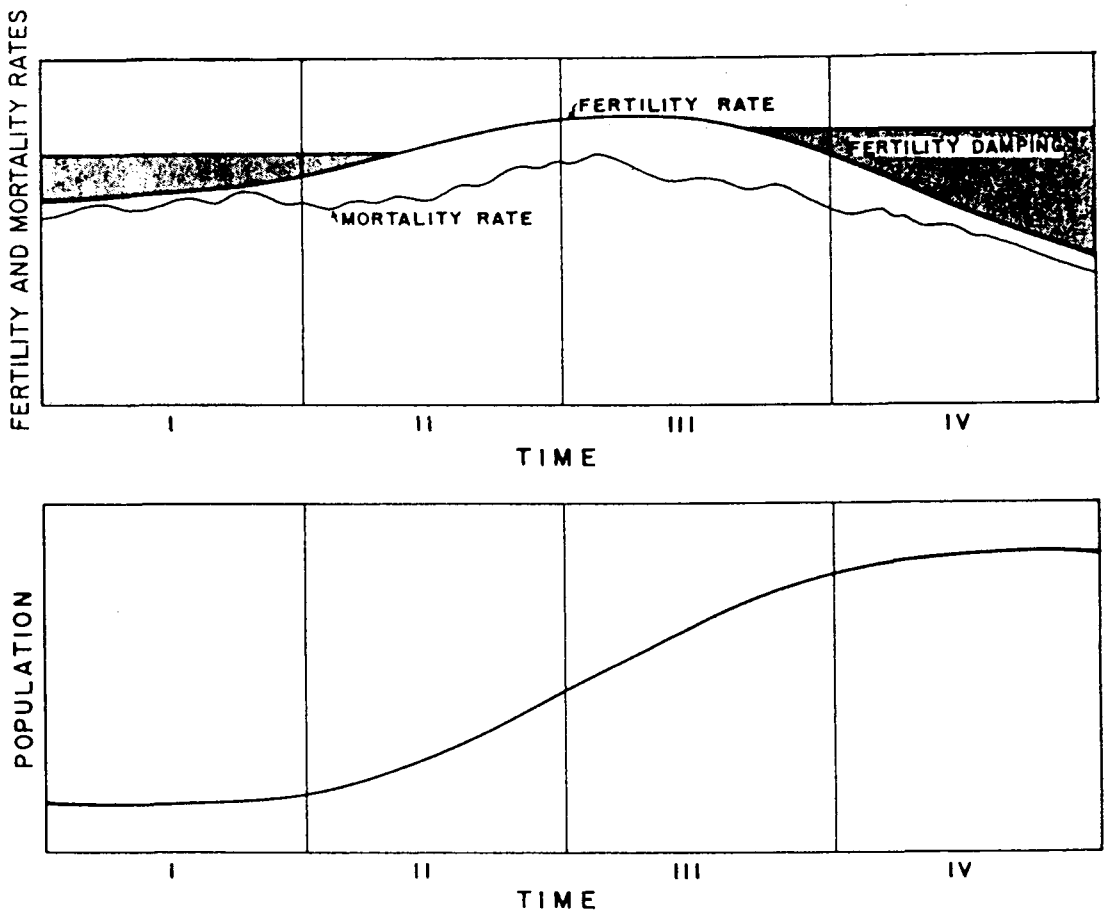

Fig. 5. The agricultural demographic transition - model (Hassan 1981).

We believe, that demographic alterations observed in pre-industrial England were not typical of the transition to agriculture.

Biodemographic data, relating to contemporary hunters and gatherers and also pre-industrial populations (agriculturalists) prove, that the interbirth interval among early agriculturalists could be twice as short as among hunters and gatherers at similar mortality structures (Trinkaus & Tompkins 1990).

Hassan (1981) suggests, that the agricultural demographic transition was caused mainly by the fertility increase at the slow changes in mortality structure (Stage II) and strong changes in Stage III (Fig. 5).

At the fertility increase in agricultural populations new effects of natural selection operating by differentiated fertility could become evident. In populations of high fertility the variance of offspring's number in complete families happens to be very high, which can cause a great opportunity for natural selection operating by differential fertility (Fig.8).

High fertility can cause two effects:
(a) mortality increase in pre-reproductive period (children);
(b) genetic variability increase in population and in this connection - the increase of number of individuals, that react phenotypically stronger in a case of changes of environmental conditions (changes caused by factors altering environmental conditions, but not eliminating individuals from a group).

Effects of increased ecosensitivity in post-Palaeolithic populations are nowadays recorded in the research of morphological stresses in skeletal populations.

Two models of adaptive strategy

General characteristics of the Palaeolithic and post-Palaeolithic adaptive strategy are listed in Table 1. It is patterned after the model for r-selection and K-selection by Pianka (1970, 593). The characteristics of two adaptive strategies correspond to the definitions proposed by Pianka.

Table 2 represents characteristics of biological traits or trait complexes in two types of adaptive strategy. The greater feature intensity is designated as plus sign.

Some detailed data concerning particular features are presented in the Figures 9 to 14.

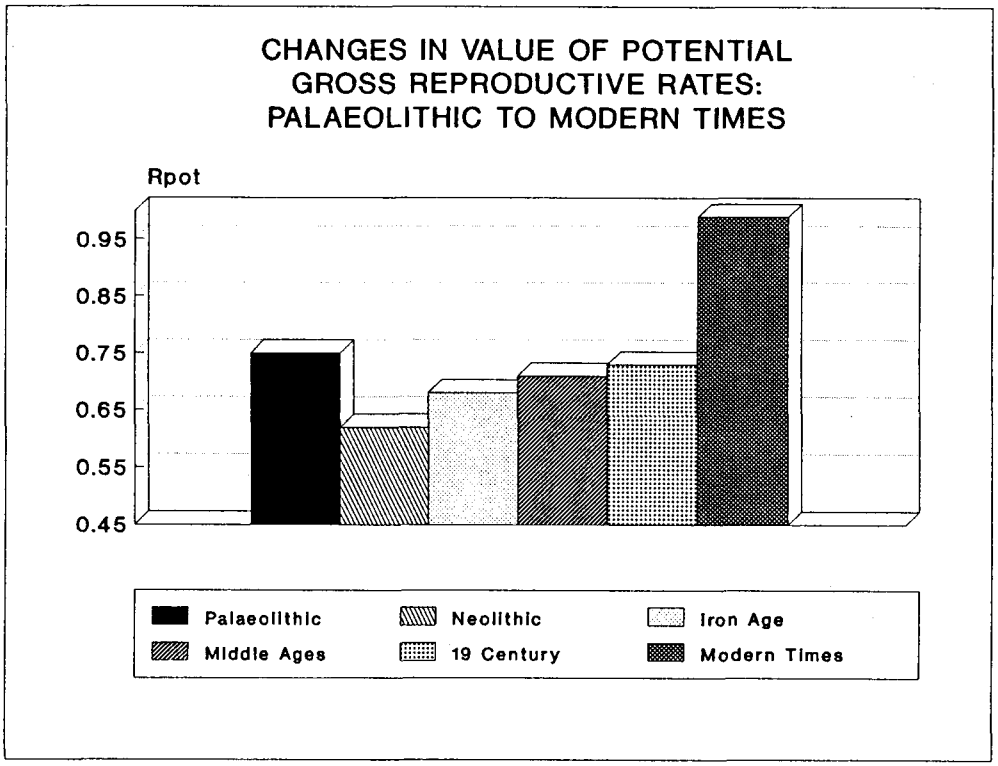

Fig. 6. Changes in value of potential gross reproductive rates: Palaeolithic to modern times.

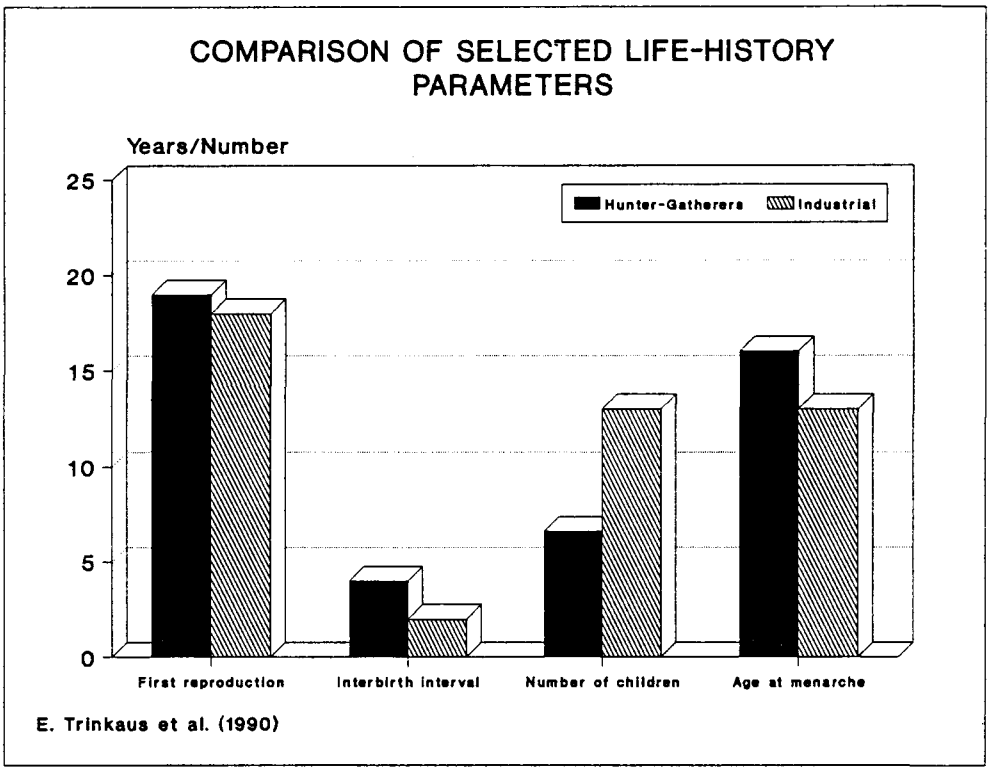

Fig. 7. Comparison of selected life-history parameters (Trinkaus & Tompkins 1990).

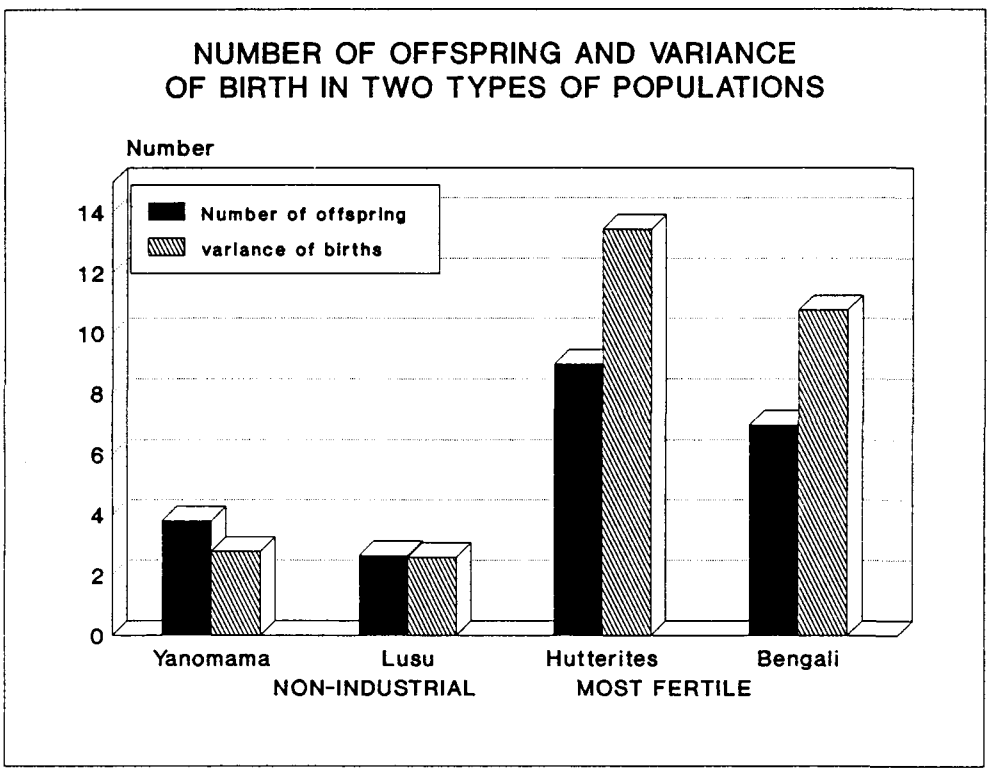

Fig. 8. Number of offspring and variance of birth in two types of populations.

Table 2. Characteristics of biological traits or trait complexes in two types of adaptive strategy. (Data from different papers)

Traits or trait complex	Palaeolithic populations	post-Palaeolithic populations
Body build		
Stature	+	-
Skeletal robusticity	+	-
Bone size	+	-
Muscle growth	+	-
Dental size	+	-
Dolichocephalization	+	-
Sexual dimorphism		
Cranium	+	-
Long bones	+	-
Palaeodemography (and biodemography)		
Fertility	-	+
Mortality	-	+
- total	-	+
- children	-	+
- reproductive period	+	-
Interbirth interval	-	+
Number of children in family	-	+
Natural increase	-	+
Palaeopathology		
Periosteal reactions	-	+
Dental caries	-	+
Hyperostosis	-	+
Infectious diseases	-	+
Harris lines	-	+
Enamel hypoplasia	-	+
Physiological stress	-	+
Porotic hyperostosis	-	+
Degenerative joint diseases	+	-
Meachanical stress reaction	+	-
Muscular hyperfunction	+	-
Ontogenetic process		
Reduced muscle activity	-	+
Reduced muscle growth	-	+
Reduced bone growth	-	+
Regularity process of growth	+	-
Reduced age at menarche	-	+

Conclusions

1. The most described morphological changes in Palaeolithic populations can be of adaptive character.
2. Numerous morphological alterations in post-Palaeolithic populations are of adaptability (ecosensitive) character.
3. The transition to agriculture changed ecological and biological characteristics of human populations. The ecological approach suggests, that the main relation of natural environment - human population - economic structure was altered. The biological approach suggests, that the criteria of adaptation and the way of natural selection operating were altered:

(a) On the ground of palaeodemographical and biodemographical data analysis of modern hunter-gatherers and agriculturalists' groups and morphological data it was shown, that in Palaeolithic differential mortality structure (particulary in the reproductive period) could be the main field of natural selection operating,

(b) In post-Palaeolithic populations a severe mortality decline is not observed. The rapid increase of Neolithic populations density, as in subsequent periods, suggests a considerable increase of fertility. We consider that just differential fertility and differential mortality in childhood could be the field of natural selection operating in these populations.

(c) The adaptation of Palaeolithic populations was forced mostly by the system of the following factors: change of ecological zone or climatic alteration in occupied ecological zone caused adaptive transformations of morphological structure.

(d) The adaptation of post-Palaeolithic populations was forced mainly by the system of the following factors: the ecological zone was characterized by relatively stable ecological conditions, which inhabited need of strong morphological adaptation. A considerable increase of fertility became evident, so as a great differentiation of descendents' number between individuals.

(f) The different way of natural selection operating could be connected with other criteria of adaptation. In these populations the individuals' ecosensitivity and morphological structure meeting new living conditions became an important adaptive criterion, so morphological processes of structural reduction (body size reduction, gracilization, sexual dimorphism etc.) increased.

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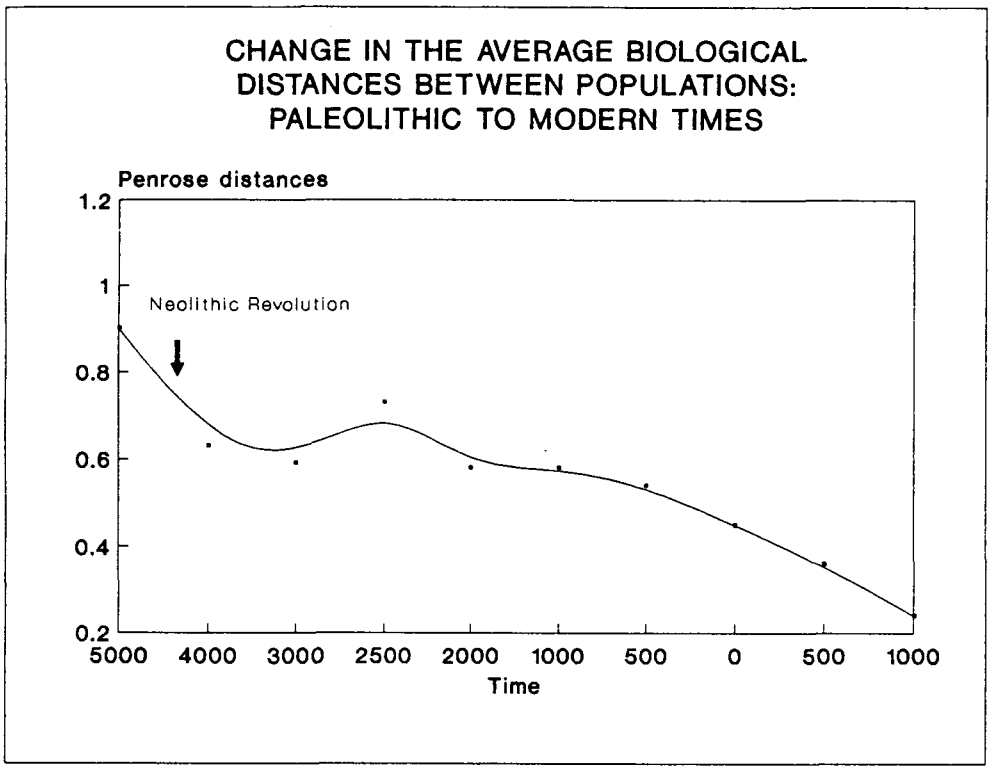

Fig. 9. Changes in the average biological distances between populations (Piontek 1979).

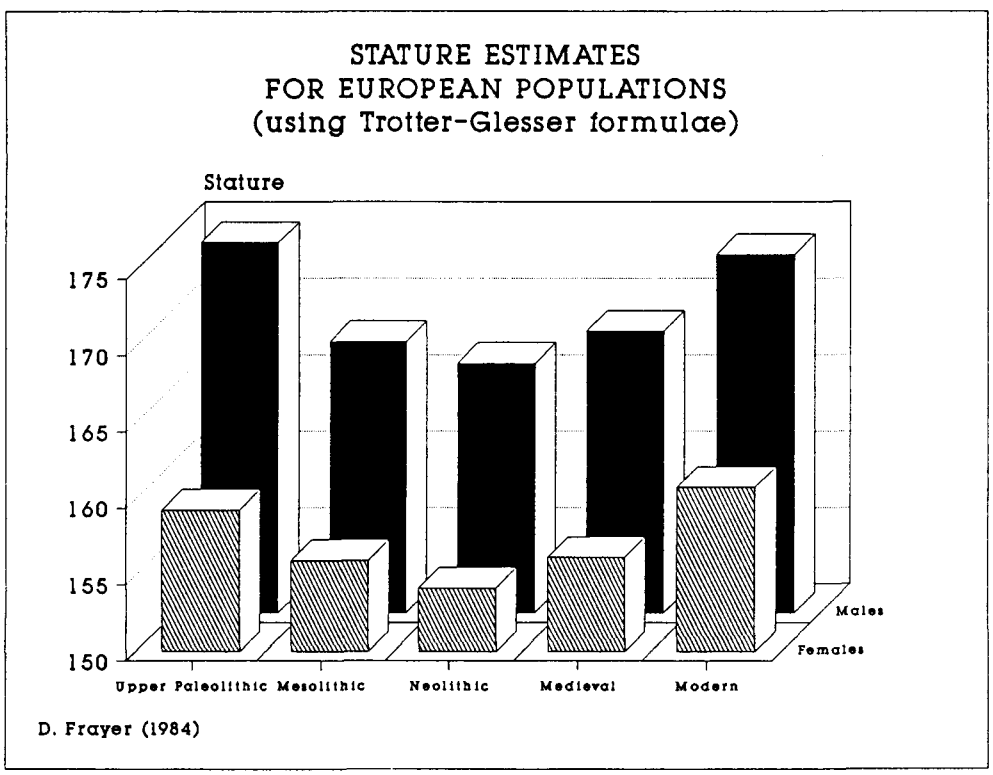

Fig. 10. Stature estimates for Palaeolithic and post-Palaeolithic populations from Europe (Frayer 1984).

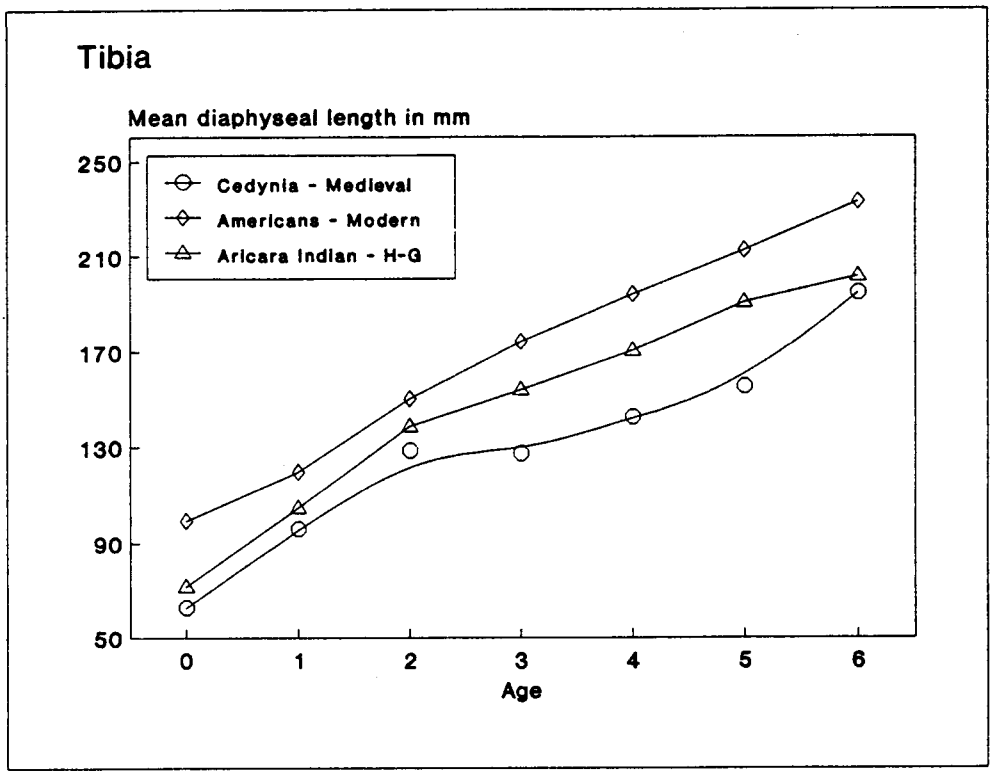

Fig. 11. Growth of diaphyseal lenght in three types of populations.

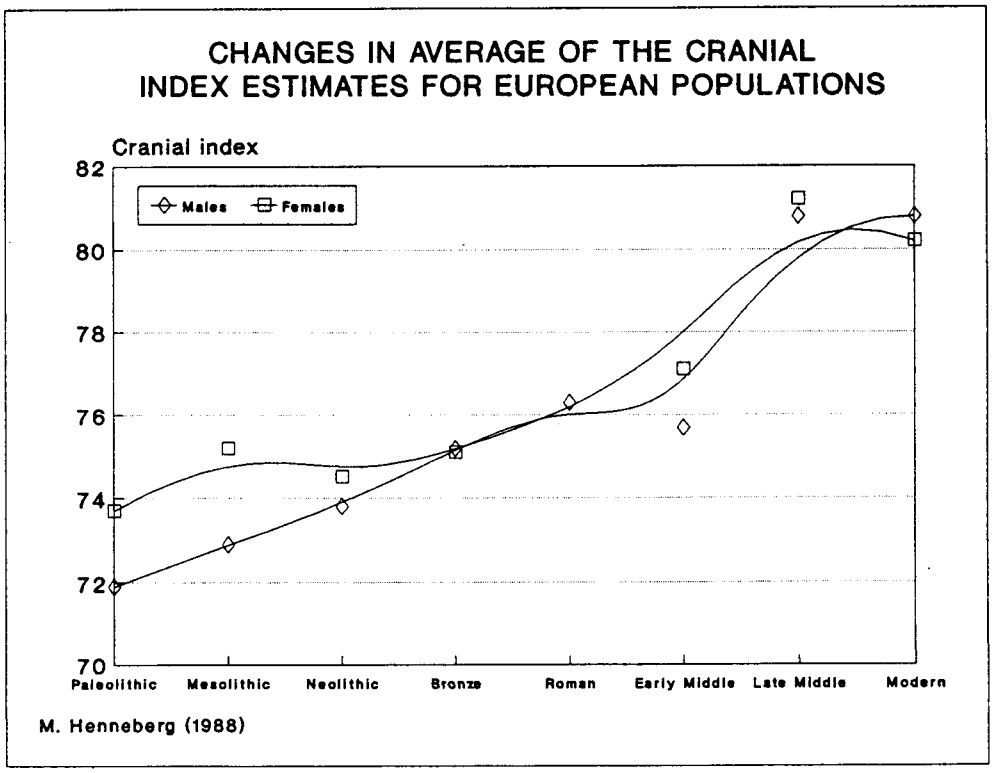

Fig. 12. Changes in average of the cranial index estimates for European populations (Henneberg 1988).

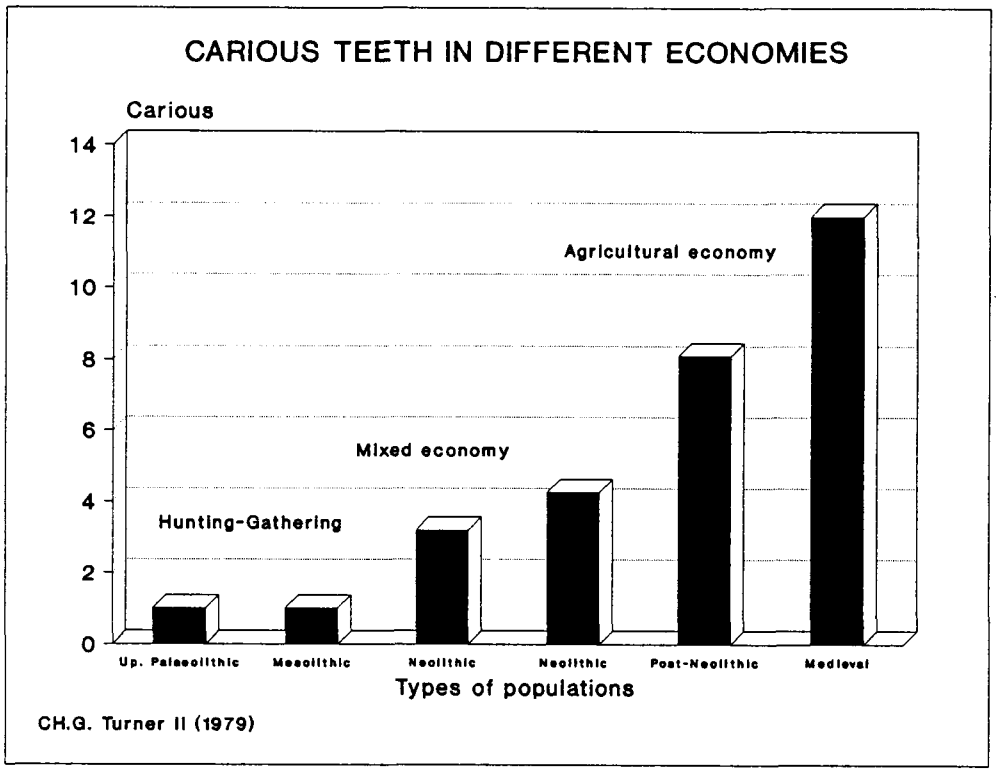

Fig. 13. Carious teeth in different economies (Turner II 1979).

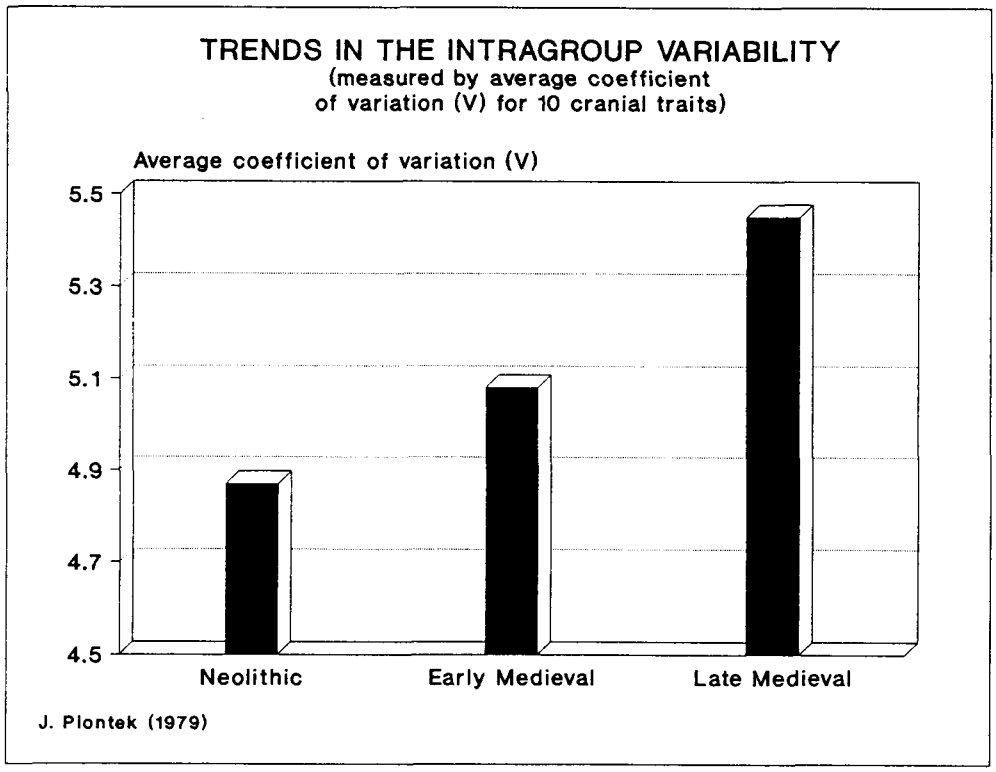

Fig. 14. Trends in the intragroup variability (Piontek 1979).