



Natural Selection and Morphological Variability: The Case of Europe From Neolithic to Modern Times [and Comments and Reply]

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Natural Selection and Morphological Variability: The Case of Europe from Neolithic to Modern Times¹

by Maciej Henneberg, Janusz Piontek, and Jan Strzałko

THE QUESTION OF THE INTRASPECIFIC differentiation of mankind may be answered in two ways. The first answer is a typological one, based on the assumption that evolutionary forces, especially natural selection, do not act upon man now that he is equipped with culture as an adaptive mechanism. Hence the human "races" developed in the Paleolithic have remained unchanged up to our time, and all the changes in the phenotypic characteristics of populations are due to gene flow and environmental factors only. The second answer takes into account all the phenomena known to population genetics, as well as knowledge of cultural evolution and the interrelations between man and the environment he creates. It is obvious that in this concept there is no room for speculation about an absence of biological evolution caused by cultural development. Man is continuously adapting to his environment, both biologically and culturally,

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but cultural change is at the same time change in the environment, demanding further adaptation. Hence he has to adapt biologically both to the natural environment and to the environment created by socioeconomic progress.

It seems that natural selection is the main mechanism responsible for the origin and maintenance of man's variability. Although numerous attempts have been made to show substantial effects of genetic drift or inbreeding on human populations, only a few rather exceptional cases of isolates, on islands, in high mountains, etc., have been found. Obviously these populations are not typical for our species at any level of cultural development. Moreover, it seems that considerable exchange of genes between populations is the normal state of human breeding groups and isolation is mostly relative, due to distances (cultural and/or geographic) separating population clusters. Hence in this paper we will deal with the effects of natural selection on inter- and intragroup variability in man.

The operation of natural selection on man may be arbitrarily

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The three authors have worked together since 1974 in a research program on the biological history of human populations, the details of which are spelled out in "Anthropology and Biological Changes of Human Populations," by Strzałko, Piontek, and Henneberg (*Przegląd Antropologiczny* 41:159-72). Other joint products of the program include "Theoretico-Methodological Presuppositions and Possibilities of Investigating the Biology of Prehistoric Populations in Central Europe," by Henneberg and others (*Przegląd Archeologiczny* 23:187-231), *Wstęp do ekologii populacyjnej człowieka* (Introduction to Human Populational Biology), by Strzałko, Henneberg, and Piontek (Poznań, 1976), and "Durability of Living Systems: Origin and Role of Culture" (*Poznańskie Studia z Filozofii Nauki*, in press).

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divided into two modes: differential mortality and differential fertility (Crow 1958). In a previous paper (Henneberg and Piontek 1975) we have discussed the importance of these two modes. Here it will be sufficient to mention only that during the vast majority of our evolution, cultural and natural regulation of selective forces was effectuated mainly by the regulation of mortality; fertility regulation, although present in all populations, did not have much connection with the genetic endowment of parents or children.

The only reasonable way to measure total selection intensity in earlier human populations is to observe the opportunity for selection resulting from mortality. For this purpose, the biological-state index (I_{bs}) is useful. The concept of biological state and the details of its measurement have been discussed elsewhere (Henneberg 1975, Henneberg 1976a, Ward and Weiss 1976). Here we will give only a brief definition and the formula for calculation of the index.

The notion of biological state relates to the notion of average fitness. We have defined it as follows (Henneberg and Piontek 1975:193): The biological state of a population is equivalent to the general intensity of selection pressures acting through mortality on all its individuals. A measure of biological state, thus understood, is provided by a quantity expressing what fraction of a given generation has a chance to participate fully in producing the next generation under given mortality conditions. This is a measure of the chance of reproductive success of the population as a whole or, equivalently, of its average individual. The greater the probability, in a given population, of complete reproduction of an average genotype, the better is the population's adaptation to the complexity of its environmental conditions. Biological state is thus an expression of adaptation, taken as the totality of biological and cultural characteristics that permit, though they do not necessarily cause, the reproductive success of a population. With regard to man we can speak only of the chance to reproduce, not of the absolute reproductive intensity, as a good measure of biological state. This is because of man's capacity, unique in the world of living beings, for conscious birth control.

The measure I_{bs} combines mortality structure with the shape of the fertility function. This shape is expressed in the form of s_x coefficients—the relative, cumulative numbers of births for age x subtracted from unity. Thus the s_x coefficient expresses the probability that the average individual of age x does not have all the progeny attainable throughout his/her entire reproductive life span. It should be stressed that the relevant s_x values are practically identical in all non-Malthusian populations, despite differences in total fertility rates among these populations (Henneberg 1975). Obviously, as follows from the definition, the values of s for $x = 0-14$ years are in fact 1, and for ages after the cessation of reproductive activity (i.e., after about 50 years of age) they approach 0, while throughout the reproductive life span the values decrease logistically with age.

The formula for I_{bs} is

$$I_{bs} = 1 - \sum_{x=0}^{x=\omega} d_x s_x,$$

where d_x = death frequency by age and ω = the age at death of the oldest member of the group.

The similarity of s_x coefficients in populations not practicing birth control in the modern form allows us to use for skeletal material the one "standard" series of s_x coefficients established on data for living non-Malthusian populations (Henneberg 1975).

Through the use of this index, we have found, for Europe and its environs, that average intensity of selective pressures consistently dropped from the Paleolithic to modern times. On the basis of these observations, we have formulated two hypotheses concerning changes in inter- and intrapopulation variability in the last few millennia. In formulating these hypotheses, we have assumed that intensity of natural selection

is the most significant factor responsible for morphological changes as revealed by anthropometric studies. Effects of migration seem less important, because throughout the period studied the isolation of human groups in Europe was only relative and gene flow was constantly present in such a range of intensity that the influence of changes in it on trends of morphological variability may be ignored.

The hypotheses are as follows:

1. Decrease in the intensity of natural selection resulted in an increase in intragroup variability of characters with a polygenic mode of inheritance.

2. Decrease in the intensity of natural selection, together with growing similarity of cultural demands under conditions of incessant gene exchange, resulted in a decrease in inter-population differences—decrease in intergroup variability of average values of characters with a polygenic mode of inheritance and greater morphological similarity of various groups.

Hypotheses such as these are acceptable on the following methodological premises: If one is aiming at the formulation of a rule describing a general natural regularity, one should first specify the variables in the order of their significance (this stage is called the construction of a hierarchy of essentiality) and then select the variable of the supposed greatest significance for the regularity in question, ignoring the rest (this procedure is called idealization). The idealized formulation of the rule is then tested against an "experimental" situation. Obviously, the corroboration will be only approximate because of the complicated structure of reality. When the corroboration, even admitting its approximate character, is not satisfactory, the investigator must take into account other variables of decreasing significance and make appropriate amendments in the formulation of the rule (this process of diminishing the degree of idealization is called concretization). This reformulated hypothesis is again tested in an empirical situation. The idealized formulation of a rule can be taken as a good description of reality when predictions derived from it do not significantly differ from phenomena observed in empirical situations (for methodological details, see Nowak 1975).

The aim of this paper is, in accordance with this methodological approach, to corroborate the two hypotheses just presented with regard to skeletal materials from Europe through the use of routine anthropometric techniques. We have taken a random sample of data on skeletal materials from typical anthropological publications concerning collections of excavated skeletons. Since published metric data on skeletal materials very often do not contain sufficient information on mortality parameters and good paleodemographic analyses are often unaccompanied by morphological descriptions, we are forced to adopt an indirect approach. This method, instead of observing correlations of I_{bs} with metric data variability for the same groups, assumes that, omitting effects of mass migrations, average intensity of selective pressures and average statistical parameters for metric characters are typical for a given territory in a certain period. Hence I_{bs} and morphological characters may be observed separately on different local groups from the same period, culture, and territory without serious risk of obtaining biased conclusions concerning the hypotheses tested.

The choice of material for study was made according to certain rules:

1. Each series of cranial measurements must represent a single breeding population.

2. The influence of random factors on statistical measures of dispersion must be minimal (e.g., the series must be sufficiently large).

3. The numbers of series representing various periods should be similar and their territorial distribution representative for Europe and its environs.

4. Individuals in the series, and series as units, must be selected randomly as representative of breeding populations, cultures, and territories.

TABLE 1

SERIES OF SKELETAL MATERIALS ANALYZED

PERIOD AND SERIES NUMBER	SOURCE
Neolithic	
12 (Russe)	Boev 1972
16	Gałasinska-Pomykoł and Szewko-Szwaykowska 1967
18 (Kara Depe)	Ginzburg and Trofimova 1972
19 (Geoksjur)	Ginzburg and Trofimova 1972
29 (<i>ceremika sznurowa</i>)	Miszkievicz 1958
30 (undeformed skulls)	Özbek 1974
31	Parenti 1965
32	Patte 1971
38	Rakowsky and Roudenko 1914
44 (Bilcze Złote)	Stojanowski 1948
46	Surnina 1963
54 (Helwan)	Wierciński 1965
57	Żejmo-Żejmis 1938
Bronze and Early Iron Ages	
3 (Staryje kiški)	Akimova 1968
4 (Kamyšly-Tamakskij mogilnik)	Akimova 1968
23	Kapica and Łuczak 1971
25 (Turan II)	Kozincev 1972
49	Ullrich 1972
56 (Širokinskij mogilnik)	Zinievic̄ and Kruc 1968
Early Middle Ages	
2 (Birskij mogilnik)	Akimova 1968
7 (Wiatycze I)	Aleksiejewa 1966
8	D'Amore and Moraldo 1973
9	Bach and Bach 1971
10	Bartucz and Farkas 1958
13	Bottyan 1972
14	Chodźajov 1969
15	Éry 1967
26	Lipták and Farkas 1967
35	Popovici 1972
40	Salivon 1971-72
41	Schott 1967
43	Stloukal and Hanáková 1974
45	Strzałko 1970
50	Toth 1964
51	Thurzo 1972
52	Vladárová-Mojžiševá and Hanulik 1970
55	Wokroj 1973
15th to 18th century	
1 (Mavljutovskij mogilnik)	Akimova 1968
5 (Siebież)	Alekseev 1969
6 (Durbe)	Alekseev 1969
11	Belniak et al. 1961
20	Gralla and Krupiński 1966
21	Hanulik and Plachá 1965
22	Kaczanowski 1965
27	Lotterhof 1968
33	Popovici 1973
34	Popovici 1973
37	Rabischong and Engel 1970
39	Salivon 1971-72
Modern times	
17 (Gložan)	Gavrilović, Stajić, and Rumenić 1965-66
24 (Walsers I)	Kaufmann, Hägler, and Lang 1958
28	Malinowski 1975
36 (Irakleios)	Poulianos 1971
42 (Żyglin)	Sikora 1956
47	Susanne 1971
48	Swornowski 1975
53 (Izvoarele)	Vlădescu 1973
58 (Konin)	authors' unpublished data

NOTE: Where only one of several series was taken from a given source, the name of the series is indicated.

Applying these rules, we took from the literature data on 58 series (table 1). We chose for analysis the following cranial measurements: skull length (g-op), breadth (eu-eu), and height (ba-b), upper face height (n-pr), bizygomatic breadth (zy-zy), minimum frontal breadth (ft-ft), length of nose (n-ns), breadth of nasal aperture (BAP), breadth of orbit (mf-ek), and height of orbit (HO). In some series the data were incomplete, so for almost all characters we have slightly different numbers of observations. This is mainly because of the requirement that, in a given series, the number of individuals with a certain character be more than ten of each sex—only the data meeting this condition were considered. More serious difficulties arose as to the choice of series representing modern populations, because collections of skeletons do not represent local groups, and, on the other hand, not all the cranial characters analyzed here can be measured on living individuals. Moreover, data from national anthropological surveys usually cover too large a territory to represent a single breeding population. In the end, we considered for analysis only six measurements (g-op, eu-eu, zy-zy, n-pr, n-ns, ft-ft) on living adults from modern local groups.

As may be seen in figure 1, the geographical distributions of series are similar in all periods, the mean distance between series in each period varying from 1,000 to 2,000 km. The smaller number of series representing Bronze and Early Iron Ages is obviously due to the fact that cremation was widespread in those periods.

Since the rate of decline of selective pressures depends on progress in culture, but not on geological time, we have used a time scale on which equal values are assigned to the distances between the following periods of cultural development: Neolithic, Bronze, and Early Iron Ages, Early Middle Ages, 15th to 18th century, Modern Times. Application of such a time scale allows us to obtain linear correlations between time, intensity of selective pressures, and variability.

Our first hypothesis states that intragroup variability of polygenic characters increases with decrease in selective pressures acting through mortality. To test this, for all analyzed characters jointly, we have computed for each series separately for males and females an average, standardized value of observed standard deviations, $m_{(s)j}$. The standardization was accomplished according to the following formula:

$$m_{(s)j} = \frac{1}{k} \sum_{i=1}^k \frac{s_{ij} - \bar{s}_i}{\sigma_{s_i}}$$

where k = number of characters in a series j ;

\bar{s}_i = standard deviation of an i th character in the j th series;

s_i = mean standard deviation of the i th character in the whole sample of series

$$= \frac{1}{N} \sum_{j=1}^N s_{ij};$$

and σ_{s_i} = standard deviation of s_{ij} values

$$= \sqrt{\frac{1}{N} \sum_{j=1}^N (s_{ij} - \bar{s}_i)^2}$$

The correlation of $m_{(s)}$ values with cultural time (fig. 2) is very clear: $r = +0.452$ (significant at the 0.01 level). From table 2 it can be seen that almost all characters, analyzed separately, behave in accordance with the general statement. Because of the relatively small number of series analyzed, only a few characters have statistically significant, positive coefficients of correlation, but even among characters insignificantly correlated the surplus of plus over minus signs is considerable and not random (significant at the 0.01 level).

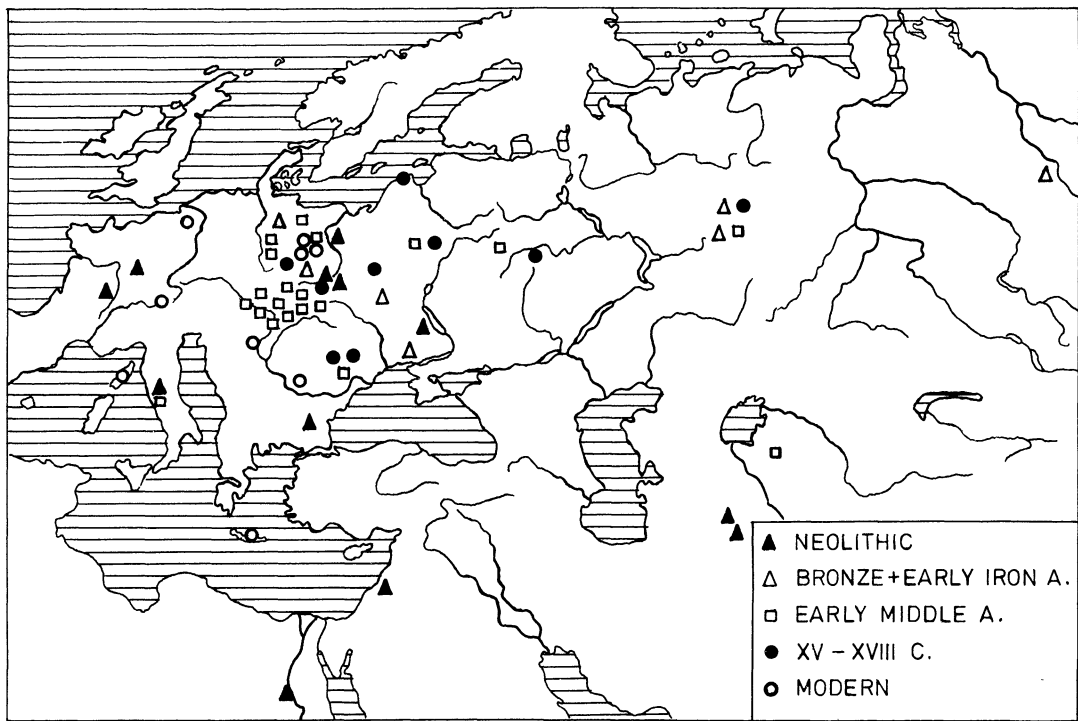


FIG. 1. Geographic distribution of the series analyzed.

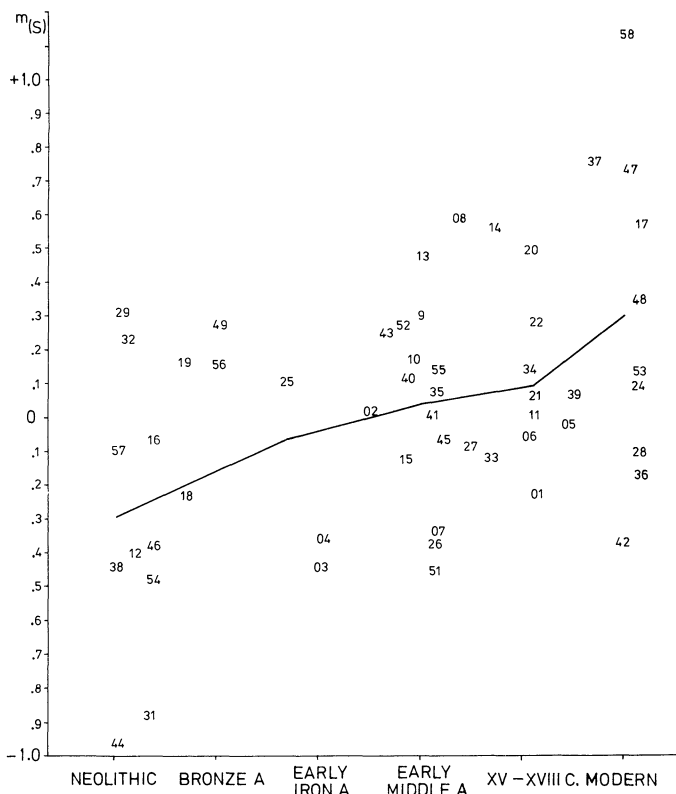


FIG. 2. Correlation between standardized measures of intragroup variability ($m(s)$) and time. Numbers refer to series listed in table 1.

The mean values of $m(s)$ and of I_{bs} , shown in figure 3, strongly suggest a coincidence between increase in intragroup variability and decrease in the intensity of natural selection, as stated in the first hypothesis.

For some of the cranial characters analyzed, there are well-known directional changes of mean values over the centuries that are imprecisely labelled "secular trends." For at least two

TABLE 2

PRODUCT-MOMENT CORRELATION COEFFICIENTS OF STANDARD DEVIATIONS FOR CRANIAL CHARACTERS, WITH TIME EXPRESSED IN UNITS OF CULTURAL CHANGE

CHARACTER	MALES		FEMALES	
	<i>N</i>	<i>r</i>	<i>N</i>	<i>r</i>
g-op.....	58	+0.256*	46	+0.075
eu-eu.....	57	+0.164	44	+0.160
n-pr.....	49	+0.370**	38	+0.456**
zy-zy.....	49	-0.215	37	+0.057
n-ns.....	50	+0.180	38	+0.212
BAP.....	43	+0.292	32	+0.194
HO.....	45	+0.348*	34	+0.250
mf-ek.....	42	+0.300*	33	+0.134
ba-b.....	39	+0.229	30	-0.128
ft-ft.....	53	+0.292*	42	-0.002

NOTE: *N* = number of groups; * = significant at the 0.05 level; ** = significant at the 0.01 level.

of these—head length and breadth—there is good evidence that the process (brachycephalization) is caused by the operation of natural selection (Bielicki and Welon 1964, Henneberg 1976b). Briefly, we may suspect that the average values of cranial characters will change under the operation of natural selection in two ways: Firstly, if developing culture changes the direction of selective pressures in the majority of breeding populations in the same way, a so-called secular trend will occur. Secondly, if cultural development is relaxing selective pressures, gene exchange among populations is present, and the cultural demands on particular populations tend to be similar but population means of given characters are close to the optimum value for a given eco-cultural situation, there will be only an increase in morphological similarity among populations—a decrease in intergroup variability of mean values without any directional change.

For purposes of analysis, we have taken mean values of characters in separate series as individual data and computed, for each period, means (\bar{X}_z) and standard deviations (s_z). In

order to maintain large enough samples, we have been forced to group data for Neolithic, Bronze, and Early Iron Ages. When looking for a trend in mean values, it is better to calculate the crude mean of arithmetic means for separate series than the weighted mean for the period, because the numbers of particular series of data do not correspond in the slightest degree with actual sizes of living populations. From table 3, it may be seen that directional change occurs in three dimensions of the brain case (g-op, eu-eu, ba-b) and upper face height in both sexes and in bizygomatic breadth in males only; in the other characters examined, there are no significant changes in mean values over time. In almost all characters, however, there is a clear decrease in intergroup variability: $s_{\bar{x}}$ values decrease with time. One may suspect that the decrease is simply a result of the increase in series size, which diminishes the proportion of

random-error variance (size of the standard error of particular mean values) in the total variance observed as $s_{\bar{x}}^2$. To eliminate the influence of this fact, we have computed a correcting factor in the form of the average squared standard error of mean values for each period and, by subtracting this factor from $s_{\bar{x}}$, have obtained estimations of the "pure" variance of mean values, $\hat{s}_{\bar{x}}$. These values, together with the results of the *F* test, are given in table 4. In order to combine the results for all characters in a single numerical value, indices $R_{\hat{s}}$ were computed:

$$R_{\hat{s}(p)} = \frac{\hat{s}_{\bar{x}(p)}}{\hat{s}_{\bar{x}(\text{Neol.})}}$$

Both the results of the *F* test and the mean $R_{\hat{s}}$ values show that interpopulational variability of cranial characters decreases with time, in accordance with our expectations.

We are well aware that the indirect method applied here permits us to draw conclusions only with a certain degree of probability. In such a situation, all possible systematic factors which could influence trends of variability without changes in the operation of natural selection should be controlled for in further investigations.

The trends of variability revealed in this study, if natural selection does not fully account for them, might be caused by the increasing mobility of people with cultural progress. In our sample of series, the influence of gene exchange on the observed trends is scarcely probable, because even abundant gene flow among groups existing in similar cultural and natural conditions cannot result in any considerable increase in the range of variability in a breeding population. Being subject to the same eco-cultural conditions, these populations exist under similar selective pressures. At the same time, interpopulational exchange of genes, undoubtedly present in the series analyzed, probably acted against the effects of genetic drift, inbreeding, etc., phenomena which may influence the variability of polygenic characters.

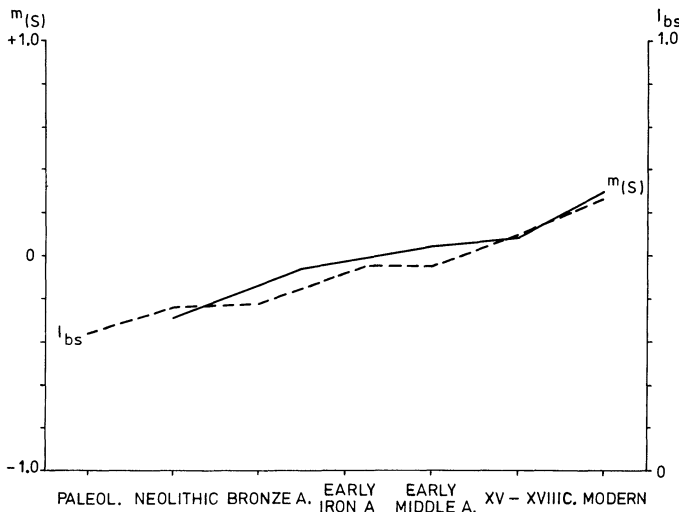


FIG. 3. Concordance between changes of mean values of $m(s)$ and I_{bs} with time.

TABLE 3

INTERGROUP VARIABILITY AND MEAN VALUES OF CRANIAL CHARACTERS WHEN ARITHMETIC MEANS FOR SEPARATE SERIES ARE TREATED AS UNITS OF STATISTICAL OPERATIONS

	NEOLITHIC, BRONZE, AND EARLY IRON AGES			EARLY MIDDLE AGES			15TH TO 18TH CENTURY			MODERN ^a		
	<i>N</i>	$\bar{X}_{\bar{x}}$	$s_{\bar{x}}$	<i>N</i>	$\bar{X}_{\bar{x}}$	$s_{\bar{x}}$	<i>N</i>	$\bar{X}_{\bar{x}}$	$s_{\bar{x}}$	<i>N</i>	$\bar{X}_{\bar{x}}$	$s_{\bar{x}}$
Males												
g-op...	19	188.1	4.75	18	184.9	2.81	11	181.4	3.66	9	189.1	3.68
eu-eu...	18	139.3	3.67	18	140.7	3.39	11	144.0	3.09	9	156.7	2.93
n-pr...	15	70.0	2.02	16	69.5	2.04	11	68.9	1.35	-	-	-
zy-zy...	13	131.9	4.22	15	133.3	1.71	11	134.1	1.74	9	141.4	1.11
n-ns...	15	51.3	1.27	15	51.2	1.26	10	51.2	0.94	7	52.5	1.07
BAP...	16	25.2	0.78	16	25.0	0.53	10	25.2	0.30	-	-	-
HO...	17	32.5	0.83	16	32.6	0.64	10	32.7	0.87	-	-	-
mf-ek...	16	42.1	1.10	15	41.1	1.28	10	41.4	1.05	-	-	-
ba-b...	12	136.7	2.67	17	134.6	1.65	9	133.2	2.22	-	-	-
ft-ft...	19	96.8	1.58	17	97.3	1.36	10	97.8	0.90	6	110.2	1.72
Females												
g-op...	13	180.2	4.86	17	176.6	2.74	10	173.4	3.42	6	181.7	1.82
eu-eu...	12	135.9	4.01	17	137.0	3.16	9	139.5	3.00	6	151.6	2.25
n-pr...	9	66.5	2.58	16	64.9	1.87	9	64.8	1.68	-	-	-
zy-zy...	6	125.6	3.78	16	125.3	2.20	9	125.5	1.66	6	133.8	1.33
n-ns...	9	48.4	1.89	15	48.6	1.39	8	48.4	0.43	4	48.4	0.70
BAP...	7	24.1	0.68	16	24.4	0.66	8	24.0	0.39	-	-	-
HO...	11	32.2	0.86	15	32.6	0.64	8	32.4	0.46	-	-	-
mf-ek...	10	40.3	1.44	14	39.5	1.06	8	40.1	0.82	-	-	-
ba-b...	7	131.4	3.62	15	129.1	1.46	8	126.8	2.02	-	-	-
ft-ft...	13	94.3	1.96	17	94.3	1.76	8	94.5	1.46	4	107.2	1.49

NOTE: *N* = number of series.

^a Measurements on living individuals, not corrected for thickness of soft tissues (all characters).

TABLE 4

INTERGROUP VARIABILITY IN VARIOUS PERIODS AS EXPRESSED BY STANDARD DEVIATIONS OF MEAN VALUES FOR SEPARATE SERIES, CORRECTED FOR POSSIBLE INFLUENCE OF SERIES SIZE

	NEOLITHIC, BRONZE, AND EARLY IRON AGES		EARLY MIDDLE AGES		15TH TO 18TH CENTURY		MODERN		<i>F</i>
	\bar{s}_x	R_s	\bar{s}_x	R_s	\bar{s}_x	R_s	\bar{s}_x	R_s	
Males									
g-op.....	4.49	1.00	2.56	.57	3.51	.78	3.64	.81	3.07*
eu-eu.....	3.48	1.00	3.24	.93	3.00	.86	2.89	.83	1.37
n-pr.....	1.69	1.00	1.93	1.14	1.13	.67	—	—	2.82*
zy-zy.....	3.98	1.00	1.30	.33	1.50	.38	.98	.25	15.89*
n-ns.....	.93	1.00	1.15	1.24	.79	.85	1.01	1.09	2.04
BAP.....	.65	1.00	.42	.65	.00	.00	—	—	2.37*
HO.....	.68	1.00	.50	.74	.78	1.15	—	—	2.52
mf-ek.....	.99	1.00	1.22	1.23	1.00	1.01	—	—	1.52
ba-b.....	2.33	1.00	1.22	.52	2.06	.88	—	—	3.75*
ft-ft.....	1.22	1.00	1.13	.93	.62	.51	1.65	1.35	3.74*
mean R_s		1.00		.83		.71		.87	
Females									
g-op.....	4.65	1.00	2.45	.53	3.18	.68	1.68	.36	6.93*
eu-eu.....	3.80	1.00	2.99	.79	2.92	.77	2.18	.57	2.76
n-pr.....	2.41	1.00	1.67	.69	1.52	.63	—	—	2.52
zy-zy.....	3.62	1.00	1.88	.52	1.44	.40	1.23	.34	8.69*
n-ns.....	1.77	1.00	1.22	.69	.00	.00	.58	.33	∞ *
BAP.....	.54	1.00	.51	.94	.27	.50	—	—	4.25*
HO.....	.69	1.00	.52	.75	.33	.48	—	—	4.08*
mf-ek.....	1.35	1.00	1.00	.74	.77	.57	—	—	3.01
ba-b.....	3.23	1.00	.91	.28	1.92	.59	—	—	13.67*
ft-ft.....	1.61	1.00	1.57	.98	1.33	.83	1.44	.89	1.39
mean R_s		1.00		.69		.55		.50	

NOTE: R_s denotes the relative value of \bar{s}_x in a period when \bar{s}_x for the Neolithic is taken as 1.00. Italicized values of \bar{s}_x were tested for significance of differences between them; statistically significant *F* values are marked with an asterisk (0.05 level).

It may be concluded that the influence of natural selection on intra- and interpopulational variability of morphological characters, although shown only indirectly, seems important. Furthermore, the observed trends of variability, whatever their causes, have to be considered in future investigations. They have practical significance for interpopulational comparisons in ethnogenetic investigations, especially those made with the aid of multivariate methods for computing "distances" between sets of quantitative characteristics representing populations. It seems that in all kinds of microtaxonomic work it will be easier to define a number of distinguishable Neolithic "racial types" than a number of modern ones. In other words, because of changes in the operation of natural selection due to the development of culture, and also to some extent because of migrations, differences between human races are continuously disappearing.

Comments

by KENNETH L. BEALS

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There is a time for new ideas to arrive. After years of preoccupation with stereotypic and typological norms, it is exciting to witness a rise of interest in variation itself. The task of anthropology is to explain human variation through time and space, for both biological and cultural traits. Such variation has dispersion as well as central tendency. Why groups differ in within-group and between-group heterogeneity is fully as important as (and probably more interesting than) why they vary in central tendency.

I have a few quibbles about the analysis and semantics of the present contribution. For example, socioeconomic "progress" implies a systematic improvement of the human condition.

Since the process is often disruptive, the more objective phrase "cultural evolution" is preferable.

The important thing is the hypothesis concerning the patterns of heterogeneity. My colleagues and I have been evaluating the hypothesis for several years with data collected from hundreds of ethnic groups around the world. Some of this is not yet published; I will, however, mention our general conclusions so that we can share with the present authors the rapid feedback which CURRENT ANTHROPOLOGY offers. Our interpretive difference appears to concern the relative role of selective (contrasted with cultural) causation.

Kelso (1974) anticipates the trends in question to apply to both time and space and throughout the world—at least as a statistical generality. The basis of this is the Law of Biocultural Evolution: as culture evolves, the variance within groups increases while the variance between groups decreases. In 1975, Kelso and I tested the law with heterozygosity among three blood groups. We organized ethnic groups by stage of social organization (from band, tribe, chiefdom, and state) and demonstrated that the expected patterns were indeed empirically observable. We also provided arguments that selection could not reasonably account for such observations.

Anthropometric traits may well be different. In fact, anything related to the size and shape of the body is part of its surface-area/mass ratio, and climate is known to be a selective agent which creates evolutionary trends among a wide variety of related morphological traits: head form, cranial capacity, body build, nose shape, and so forth. To agree that anthropometrics are influenced by selection does not, however, provide evidence that selection is responsible for the patterns of variation reported. More generally, trend analysis by itself will not separate the effects of natural selection from those of nonrandom mating.

As culture evolves, the probability of mating between different genotypes increases. It creates an expanding population structure in which different alleles, genotypes, mating types,

morphological traits, languages, and behaviors are more likely to be combined. It is a process of isolation breakdown, the inevitable consequence of which is to create the observed patterns of heterogeneity.

Europe from Neolithic to modern times has some cultural features which generally typify the entire world: (1) an increase in population size (which would reduce the coefficient of inbreeding), (2) more advanced systems of transportation (which increase the mobility of individuals), and (3) increased "imperialism" (by means of which variable populations come increasingly under centralized political control). If these elements of culture change are present, the result is theoretically expected to be as Henneberg, Piontek, and Strzałko have discovered. The culture change is independent of selection but produces evolutionary trends with central tendency and dispersion. Observing the trend from empirical data, one would probably be tempted to conclude that selection was the cause. It may be; it may not be. To demonstrate the affirmative requires, however, that the effect of cultural evolution be analytically separated.

We have just completed two additional studies on the same topic. From the first, we discovered that polygenic characters are generally correlated with cultural evolution around the world despite the large number of overriding influences which are probably present. In the second, we applied the theory to individual social behaviors but found no association whatever.

Our interpretive difference with the authors seems to be only a matter of emphasis. They stress selection, while we stress the cultural factors involved. We all recognize some interaction between them. We are actually dealing with a broader phenomenon of biocultural evolution in which population structure, social organization, and natural selection are intimately connected. The present study has a direct relevance to a better understanding of this phenomenon.

by DELLA COLLINS COOK

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This paper is innovative in its use of osteological data to address questions of broader interest than the local archeological sequences it includes. The authors demonstrate time trends in both selection intensity and variability.

The causal link they hypothesize between these trends is difficult to accept without further analysis of morphological and archeological data. Other attempts at demonstrating relaxed selection with time (Brace and Mahler 1971) and with relative cultural complexity (Post 1964, 1966) are similarly limited. In all three instances, it is possible that other models may provide plausible explanations for the observed trends. An example of such an alternative model omitting reference to selection follows: Increasing social and technological complexity, as reflected in "cultural time," results in increased community size through the aggregation of isolates; the breakdown of isolates results in increased within-group variability and decreased between-group variability through the effects of sample size on the sampling of a heterogeneous distribution. Under these hypotheses, the observed correlation of variance with selection intensity may be viewed as the spurious result of joint correlations with time. Similar alternative models centering on effective size of breeding populations, social stratification, mechanisms of group formation, and the like are possible. Any effective demonstration of relaxed selection must eliminate the more plausible among these alternative models through an examination of the relationship of other possible causal variables and time or cultural complexity.

The authors suggest that selection is the only important component of morphological variability in the series they employ. However, other components are demonstrable and may well be useful in explaining the trends they observe. Variance as re-

lected in bilateral asymmetry can be shown to result from environmentally mediated deviation from the canalization of development (Bailit et al. 1970, Doyle and Johnston 1977) independent of the genetic components of variability and hence of selection. Work on the Yanomamo has demonstrated that within-group homogeneity and between-group heterogeneity reflect lineage effect in the formation of new communities rather than the effects of selection per se (Chagnon 1972, Spielman, Migliazza, and Neel 1974). Since a series spanning the Neolithic-to-Modern period also spans the shift from tribal to state organization, such effects may be expected to decrease with time, hence increasing within-group variability. Similarly, the variance of anthropometric measures in the living can be expected to exceed the variance of skeletal measures on the same individuals, in that the added effect of soft-tissue variability is included. Reexamination of the results presented here omitting the living samples might be profitable.

A broader problem is presented by the assumption that skeletal collections adequately represent the variability present in the breeding population. The use of samples as small as ten individuals permits questioning of the stability of variance estimates. Furthermore, skeletal collections from archeological sites are frequently modest in size even when the community they represent was large. They are seldom representative of the range of disposal contexts used by the community or of the social groups present within the community. In many instances excavations may be biased toward the inclusion of related individuals, through inclusion of family plots, or toward particular classes, moieties, or economic groups. From Neolithic to Modern times, European communities can be expected to have changed dramatically in size, effective size of the breeding population, social stratification, mortuary practices, and, most importantly, the degree to which residence and burial were kinship-based. All these factors limit the appropriateness of variance in a skeletal collection as a measure of variance in the population it represents. It is by no means obvious that these effects will operate similarly in all the time periods sampled. A discussion of archeological information on the samples included in this study, encompassing sample size, community size, and nature of mortuary units and practices, could clarify the importance of these effects through time. Such a discussion could strengthen the interesting argument the authors present.

by JOHN HUIZINGA, TRINETTE S. CONSTANDSE-WESTERMANN, and CHRISTOPHER MEIKLEJOHN

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The study of Henneberg and colleagues raises both analytical and theoretical questions. The results obtained are not clearly related to the reasons given. We would like to raise some questions about the analysis and then turn to some of the theoretical assumptions.

The nature of the samples used raises two points: Firstly, whether they represent single breeding populations remains to be proven. Such proof is said to be necessary but is not attempted here. Secondly, while the various periods are said to be represented by samples of equal territorial coverage, this is not apparent when the samples are examined. No fewer than four of the thirteen Neolithic samples are non-European, compared to one of the forty-five later samples. The effect of these non-European samples can be expected to increase the range of variability in the Neolithic sample, thus biasing any results obtained. If proof for the hypothesis is required, why not use a set of strictly localized populations such as those from the Ukraine recently published by Konduktorova (1974)?

In the analysis, the assumption is made that selective pressures are linearly correlated with cultural progress. Further-

more, the periods treated are seen as involving equal degrees of cultural change, and therefore of selective pressure. Such a model of cultural development is acceptable to few prehistorians. Not only are the periods of unequal length, but the technological changes are far from equivalent. For example, the acquisition of bronze by a community is generally seen as having had little effect on the life-style of the average community member. In many cases, so-called Neolithic and Bronze Age technologies existed side by side in the same community. If the cultural levels used in the paper are not of equal magnitude, the linear correlation (fig. 2) between cultural development and the value of $m_{(s)}$ ceases to have obvious meaning. Furthermore, the plotted correlation (r) is dependent upon the series used, and the overlap in the values of $m_{(s)}$ for varying time intervals is great (the Bronze Age sample falls totally within the range of the Modern sample).

Other questions are also related to analytic matters. Is the brachycephalization noted under the control of natural selection, as stated, and therefore, by definition, genetic? Studies going back to the classic Hawaiian work of Shapiro and Hulse (1939) bring this into question. The complexity of this problem can be seen in the work of Huizinga (1958). Is there increased mobility with cultural progress over time? How far back could such an idea be pushed? Pre-Neolithic populations with low densities can be expected to show mobility related to areal constraints on the number of people required to maintain an operational breeding population (Meiklejohn n.d., Wobst 1976). Neolithic populations of increasing density would be expected to show increasingly less mobility over time. The localized population structure of agrarian populations has been demonstrated on Bougainville by Friedlaender (1975) and in Oxfordshire by Harrison and Boyce (1972). Increased mobility is hard to document except in those populations which have become urbanized. Even in Western urban society such mobility is strongly related to social class and is thereby restricted to a small section of society.

This last point directs the discussion towards more theoretical aspects of the paper. The paper is based upon a number of assumptions that are critical to the interpretation of the analysis.

Gene flow is assumed to be relatively constant across cultural levels; this has been queried above. Gene flow, closely related to the factor of density just noted, may be critical in explaining morphological variability in space at differing cultural levels (Meiklejohn 1974).

Further, it is assumed that selection occurs mainly through mortality rather than through fertility and that an individual's ability to reproduce is related primarily to mortality. The latter point underestimates cultural factors, such as polygyny, which affect the relative genetic success of different individuals in a population (Chagnon 1972). Polygyny is more likely to be seen in developed societies and is therefore of growing importance over time (Meiklejohn 1974). Simple reproductive ability is countered by such cultural systems, irrespective of any mortality profile. Even more important is the apparent under-rating of the place of fertility in selection. Recent work suggests that fertility may be a central concern in the development from pre-Neolithic through Neolithic and later systems (Cohen 1977). Lee (1972) argues for birth spacing as a major factor in population control at the band level. Howell (1976) has indicated that physiological mechanisms related to Frisch's work on critical weight may be involved. If anything, it may be fertility rather than mortality that is critical to understanding of the period under consideration, thus considerably blurring the distinction made between (theoretical) Malthusian and (empirical) non-Malthusian populations (discussed further by Henneberg 1976a). This will affect the meaning of the parameter $s_{(x)}$ and thereby the conclusion that there is a drop in the average intensity of selection pressure over time.

Further assumptions surround the importance of natural se-

lection in the maintenance of morphological variation and the ignoring of changes in the rate of gene flow. Probable changes in the rate of gene flow over time have been mentioned. The efficacy of gene flow has been well demonstrated by Brues (1972). We also query whether local populations during the earlier periods involved here would have been large enough for selection to outweigh random changes in gene frequency. It is possible to develop an alternate model in which natural selection increases in intensity while gene flow decreases during the time period under consideration. This might produce an end product opposite to that predicted in the article.

A final important assumption is that a decrease in the intensity of natural selection will result in increasing variability in measurable polygenetic characters. This may not be as simple as it seems. Bailit (1966) has demonstrated that variability in individual characteristics is *not* related to genetic variability and probably involves complex interaction with environmental buffering. Such an observation can also be seen in early work on the variability of hybrid populations (see Muller 1936, Trevor 1953). Furthermore, Bulmer (1976) has demonstrated that *genetic* variability will be affected differently depending upon whether selection is disruptive or stabilizing. Selection can, in some cases, increase genetic variability. It thus seems unwise to predict that decreasing natural selection will result, *ipso facto*, in increased morphological variability. It also remains to be demonstrated that selection pressures affecting later cultures are both lessened and increasingly similar over large geographic areas.

In conclusion, it is difficult to agree that the results obtained are necessarily due to the factors suggested. In addition, the tabular data are not in all cases consistent between males and females, and the statistical manipulations are not always clear. The decrease noted in intergroup variability may be related simply to the inclusion of non-European samples in the Neolithic group. Finally, if Neolithic racial "types" are easier to define than modern ones—a doubtful exercise in any case—this may indicate localized genetic isolation present in the later Neolithic and post-Neolithic but absent in pre-Neolithic as well as in modern urban populations.

by FREDERICK S. HULSE

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At the present time, it is more difficult to distinguish between Europeans from different areas than it used to be a long time ago. This, at any rate, is the conclusion of Henneberg, Piontek, and Strzalko, and I wouldn't be surprised if they were correct; but I searched their article in vain for positive evidence that this is due to natural selection rather than population admixture. Increased variability within local populations, for some of the cranial traits considered, seems to be a widespread trend. The authors attribute this to a decline in selective pressures due to improving technology, but it could just as readily be explained by increased miscegenation as improving technology made travel easier.

The authors state quite frankly that they *assume* natural selection to be the most significant factor in morphological change. They dismiss the effects of migration and gene flow on the grounds that, within Europe, isolation between human groups has never been absolute since the Paleolithic. This is of course true, but there are many steps between total isolation and no isolation whatever. We know that even such simple technological changes as the introduction of bicycles greatly increases the area within which people search for mates. It seems shocking to ignore the influence of migrations, which have become easier with each improvement in transport and with each expansion of empire.

Quite properly, the authors state that "each series of cranial measurements must represent a single breeding population."

We have no means of knowing, however, how they were able to assure themselves that all, or even any, of the cranial series they use do really meet this requirement. All of us who have worked with American Indian skeletal material realize the difficulty of knowing anything of the sort. And how can we know that, in times and places where cremation was widespread (but not universal), the noncremated remains we find don't represent some unusual, nontypical group? Perhaps they were enslaved captives, or members of a lower caste.

It seems to me that Henneberg, Piontek, and Strzałko have made a very ingenious attempt to demonstrate the continued operation of natural selection upon our species, at least in Europe. I have little doubt that this proposition is correct, but their assumptions are shaky and their data are dubious. Were I a skeptic, I would not be convinced.

by FRANK B. LIVINGSTONE

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For the authors' results to be due to selection, it is necessary to make the questionable assumption that the amount of gene flow has been the same for all these periods. If gene flow has increased through time, it could have produced the same results of decreased interpopulational variation and increased intrapopulational variation that they attribute to selection. My own work on hemoglobin variants has convinced me that a very small amount of long-distance gene flow is of great importance in determining genetic variation. It seems obvious to me that, with the great migrations of the Middle Ages in Europe and the subsequent invasions and crusades, both the amount and the range of migration changed considerably. Population size also influences genetic variation through gene drift, but Henneberg et al. do not discuss the very certain changes in population size through time. Finally, the models of Malécot and Wright, as applied to human populations by Morton and others, clearly demonstrate that migration pressure for most human populations is so much greater than selection pressure for most human loci that the effects of selection on human variation are too small to detect. Thus, although I still think most human genetic variation is due to natural selection, the effects of the latter cannot be measured by studies of genetic variation among human isolates. The noise is greater than the signal.

by ROLAND MENK

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Henneberg, Piontek, and Strzałko are to be congratulated for their attempt to introduce an indicator of the eco-adaptational success of historic (and prehistoric) populations. An indicator such as their I_b represents a long awaited methodological link between physical anthropology and paleodemography, which will help to establish, eventually, a more in-depth collaboration between these two branches, which—despite large zones of common interest—have never really reached a level of essential information interchange and mutual enrichment of research.

It seems necessary, however, to formulate two points of criticism aimed at the oversimplified approach to phenotype evolution—its description as well as the explanation of its causality—during the last few millennia.

First, it must be stressed that the patterns of morphological evolution are much more complex than the authors seem to suggest. This remark applies to the purported "directional" changes of general skull morphology, as well as to the time-dependent behavior of its intergroup variability. A more in-depth analysis of the European Neolithic (covering more than 4,000 years, and therefore equivalent to the time span of the authors' material) shows three time-dependent phenomena (Menk 1975): (1) gracilisation-degracilisation; (2) brachyceph-

alisation, and (3) increase of intergroup variability. These facts are clearly in contradiction with the authors' results and hypotheses. The instability (or reversibility) of the purported directional changes (morphological trends as well as oscillation of intergroup variability) is confirmed by Creel (1968) for an even longer time span.

With these arguments, I intend to show the shortcomings of the authors' model, which pretends to give a full explanation of the evolution of morphological variability in man. Being based exclusively on natural selection (essentially through differential mortality), this model is only of restricted validity: it may give fairly accurate pictures for periods of negligible population dynamics, but it inevitably fails when applied to phases of increased population movement (such as the early and late Neolithic, the early Middle Ages, etc.). For these periods, the model must account, in addition, for migrational factors and, besides elements of a genetic nature, should take into consideration the possibility of exogenous factors such as ecological and economic stress. The gracilisation-degracilisation of the European Neolithic provides a good example of the latter (Menk 1977).

Once again we are confronted with a model which, based on theoretical considerations of population genetics, reproduces reality in very particular circumstances only. For the sake of algebraic formulation and of practical application, several important factors in the evolution of variability have had to be discarded. In other words, the conceptual background had to be adapted—by declaring these factors "negligible"—to the possibilities offered by the severely restricted number of parameters available for observation and model building.

It must be conceded, however, that the task undertaken by the authors is anything but easy. In order to obtain estimations of I_b , they have had to perform several "tours de force," which have already been critically commented on by Ward and Weiss (1976:11).

Second, the authors' views on cultural evolution seem to be strongly oriented in such a way as to confer general validity on their model of morphological variability: in addition to the more biological explanations invoked, the authors refer to the idea of a general cultural convergence—another oversimplification—leading towards uniformity of selection criteria. This would further neutralise the (already reduced) effect of gene exchange. There is undoubtedly something like cultural convergence; but there is also, and at the same time, cultural diversity: there are agrarian, urban, warfare practicing, etc., cultural groups, each obeying its own laws of cultural and biological interaction. Cultural convergence is therefore confined, at least for the past, to operation essentially *inside* each of these cultural partitions, and not across them.

How are we to explain, under these circumstances of conceptual disagreement, the fact that the authors' hypotheses and results are in obvious concordance? It seems not unreasonable to suggest that their sampling strategy, through the requirement of large local series, could have led, unconsciously, to a choice of material representing a single type of sociocultural partition and/or coming from periods, or regions, of relative stability. It might be worthwhile to check the cultural and historical (political) context of each of these series in order to detect, in the form of a possible community in the postulated sense, a bias in the distribution of the material. This would mean—if these suspicions were to be confirmed—that variation of selective pressure may well explain some of the changes in morphological variability over time. Relaxation of the intensity of natural selection, as shown by means of the Index of Biological State, would be most significant in periods of biological and political stability and much less so in periods of upheaval and mass migration. The former phases, in accordance with the authors' ideas, would be characterised by reduction of intergroup variability, whereas the latter would be

responsible for regenerating it. As a whole, the pattern of intergroup variability over time would be a pulsating motion of increase and decrease, rather than the steady fading away suggested by the authors.

by MICHAEL PIETRUSEWSKY

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While I consider the approach adopted by Henneberg et al., combining methods in current use in palaeodemography with data (skull and head measurements) taken from the literature, novel and even potentially rewarding for studies of human variability, I became slightly lost between the formulation of the hypothesis and the conclusions. While I am not necessarily in disagreement with these authors' main conclusion that there has been a general increase in intragroup variability and decrease in intergroup variability with relaxation of natural selection, I do not feel that the methods and, more particularly, the data utilized in this paper support such a claim.

Despite the authors' own admission that they must argue from indirect evidence (I_{bs} and metric parameters coming from separate sources), I would like to draw attention to some possible errors which may have been introduced during the initial selection of data and samples. Specifically, how close do the authors come to satisfying the idealized criteria they enumerate at the outset?

It is stated that each series must be sufficiently large, yet all we are told is that each sample contains more than ten of each sex. Likewise, one wonders how closely any of the series utilized approaches the definition of "breeding population," or how one might substantiate such a claim when dealing with skeletal material. Similarly, the actual method of selection of samples to randomly represent breeding, cultural, and territorial aggregates is largely left to the reader's imagination. Furthermore, inspection of the map in figure 1 leaves me unconvinced that these series overlap, temporally and geographically, to the extent stated. The use of such labels as "Neolithic," "Bronze Age," "Early Iron Age," etc., to define temporal sequences encompassing Europe and its environs is almost meaningless to me. I am somewhat surprised to find that the authors combine osteometric and anthropometric data without indicating whether or not appropriate corrections were applied to the latter to make them comparable to the measurements made on bone. Finally, the unevenness of the data (ten cranial vs. six skull measurements) would seem further to limit comparisons based on already sparse data.

While I am very pleased to see an attempt to synthesize palaeodemographic and more traditional anthropometric data for addressing issues of human variability, I would caution readers against accepting the conclusions reached in the present paper until the authors can tell us more about the manner in which data and samples were selected.

by FRANCISCO ROTHHAMMER

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Henneberg, Piontek, and Strzałko's well-intentioned efforts to study temporal trends in craniofacial variability are legitimate and should probably be encouraged. However, I do not share their evolutionary interpretation, which is marked by unaffected simplicity, particularly with regard to the effects of population structure on the maintenance of genetic variability in human populations. Further, the literature cited has a parochial flavor.

There are some paragraphs which are difficult to understand. For example, the authors state that in formulating their hypothesis they have assumed that "intensity of natural selec-

tion is the most significant factor" and that "the effects of migration seem less important," but then they state that "gene flow was constantly present in such a range of intensity that the influence of changes in it on trends of morphological variability may be ignored."

The authors seem to assume, furthermore, that the genetics of the cranial measurements is well understood. Unfortunately, the mode of inheritance and the genetic determination of continuous morphological variation is, as a result of methodological difficulties, rather obscure (see, for example, Lewontin 1974).

I miss an explanation of why equal values are assigned to the distances between the periods of cultural development on "the cultural time scale" and what is gained by using this and not a simple time scale.

A correlation of 0.452 may look "very clear," but it should be considered that only 20% of the variation in $m_{(s)}$ values is explained by "cultural time." It would be interesting to ask what other factors are contributing to the variation in $m_{(s)}$ values.

The increase in intragroup variability with time may be explained by relaxation of normalizing selection, among other factors, but the decrease in intergroup variability of average values is most probably a result of increasing geographic mobility and not of a decrease in the intensity of natural selection.

by FRANCISCO M. SALZANO

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This is an interesting paper, and the authors should be congratulated for trying to extract a coherent picture from data scattered in many articles, some of them published in journals not readily available in the Western world. The limitations of the information presented and the possibility of alternative answers should, however, be clearly stated. The authors' main thesis may be briefly summarized as follows: (a) Since the Neolithic, there has been an increase in intragroup and a decrease in intergroup variability in some characteristics of human populations. (b) This has occurred because of relaxation in the mortality component of selection.

No one doubts that mortality has declined as an evolutionary factor in man; what remains to be proved is that these changes are the sole cause of the trends discernible in the characteristics chosen. First, there is very little information about the degree of genetic determination of the variability found in these traits. Selection may be acting on head form, but the fact that the picture is far from clear is lucidly expressed by Bielicki (1975). Second, I_{bs} is an index of *potential selection* only. Not all mortality has genetic implications, since accidental deaths occur everywhere. Third, intragroup variability can decrease and intergroup variability increase in the absence of selection. Fourth, the time available for the action of evolutionary factors since the Neolithic (about 500 generations) is not long.

In a way, there is a contradiction between some of the statements made and the results. The authors strongly emphasize the importance of natural selection in shaping our present variability (a position that I fully endorse) but try to demonstrate the effects of relaxed selection. If this factor is not as important as it used to be, the implication is that others (such as population size, assortative mating, or environmental influences) may be the ones that led to the observed trends. On the other hand, the assumption that selection has been relaxed in modern times does not necessarily lead to a typological approach as the authors state in their first paragraph. I also cannot agree with their position that the mortality component of natural selection has almost always been the most important in human evolution. Cultural factors undoubtedly influence fertility, but there is ample evidence for the action of biological

agents also (genes that influence sexual determination or chromosomal aberrations that cause abortions, to name just two obvious examples).

by G. RICHARD SCOTT

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Although espousing evolutionary principles, workers in the field of skeletal biology often avoid the difficulties of processual analysis for the more straightforward methods involved in phenetic distance computations, i.e., historical analysis. For this reason, Henneberg, Piontek, and Strzałko are to be commended for their attempt at discerning the influences of natural selection on the craniometric dimensions of European populations through time. There are, however, several problems associated with their methodology and interpretations.

The hypotheses formulated by the authors state that a decrease in the intensity of natural selection resulted in (1) an increase in intragroup variability and (2) a decrease in intergroup variability. From a statistical standpoint, these are alternative hypotheses. As the variation in cranial characteristics is measured through time, the null hypothesis should be that there is no change in intragroup (or intergroup) variability for characters x through time in European populations. The alternative hypothesis should specify the direction of the change or variability (increase or decrease) and an explanation of the change. "Decrease in the intensity of natural selection" is only one of several explanations that could be specified by alternative hypotheses. Either increasing population sizes or an increase in gene flow between groups could also be used to explain the detected temporal changes in intra- and intergroup variation. The analytical method employed, however, does not have the power to sort out the individual or relative effects of genetic drift, gene flow, and natural selection.

The authors summarily dismiss the possibility that genetic drift or gene flow had a significant effect on human variability in Europe. Although religious isolates and island populations are often employed to illustrate the operation of genetic drift, the effects of this process are by no means confined to such groups. As just one example, the work of Neel and his colleagues among South American Indian populations (cf. Neel and Salzano 1967, Neel 1970, Neel and Ward 1970) shows clearly that founder's effect and genetic drift generate a significant proportion of total intergroup variability. Only in a large unsubdivided population would one expect drift to have a minimal effect on gene-frequency change, and this population structure is relatively recent in the densely settled industrialized areas of Europe. Regarding the effects of gene flow, the authors imply that admixture rates were so uniform among groups that this process could be ignored. Despite this, they realize that, through time, mobility increased and enhanced gene exchange between populations. This increase in mobility and gene flow would result in an increase in intragroup variation and a decrease in intergroup variation, the same situation they attribute to a decrease in selective pressures.

Not surprisingly, the findings of Henneberg et al. are concordant with the so-called biocultural theory of Kelso (1974: 328), which states that "as culture evolves," intragroup variability increases and intergroup variability decreases. In that text and in subsequent empirical tests (Beals and Kelso 1975), the interpretation of this theory centers on temporal trends such as increase in population size, the breakdown of isolation (i.e., increase in gene flow), and decrease in level of inbreeding. Although the relaxation of selective pressures may also play some role in this changing pattern of human variability, there is still no evidence to indicate how this process contributed to the changes. While mortality patterns have seemingly been changing in parallel with the trend toward increased intragroup

variability, there is nothing in the analysis that demonstrates a direct or causal relationship such as the authors imply. The correlations measured are just as likely indicative of general trends in cultural evolution, particularly relating to change in population size and structure.

One final point pertains to the sampling procedure: The authors state that "each series of cranial measurements must represent a single breeding population." It is not clear from the text whether this limitation is spatial, temporal, or both. Cadien et al. (1974) are highly critical of attempts to discern evolutionary trends employing skeletal material because the samples generally represent *lineages* rather than temporally distinct breeding populations. Statistical characterizations of lineages contain varying degrees of bias in estimating "population" means and variances, depending on the constituent breeding populations. Unless a worker can strictly delimit the temporal boundaries of his skeletal sample, there is no way to estimate either the degree or the direction of this bias. While I would not go so far as Cadien et al., who suggest that such studies are futile, their comments should be considered in skeletal-based studies of microevolutionary change.

by C. SUSANNE

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This paper gives us an example of the multiple difficulties we encounter in studying large human groups. Though complex, this kind of study is indispensable; indeed, our modern populations are large breeding groups in which absolute isolation is exceptional.

Population genetics, in the study of relationship between demographic parameters and evolutionary processes, deals mostly with models that do not incorporate such demographic complexities as age structure; therefore the attempt of the authors is very interesting. The interpretation of the results, however, has to be made with considerable caution. The interpretation of past data in terms of present populations is difficult; it is hard to believe that cultural organization does not influence the decrease in the rate of reproduction due to different causes and/or mortality; moreover, the size of the population probably has an influence on demographic data via random fluctuations due to the small number of individuals.

I must also point out that the indices proposed by Henneberg et al. measure, not the intensity, but the *opportunity* of selection. Genetic changes due to the pressures of selection only occur when the differences of mortality and fertility are related to (or are specific for) genotypes. The relationship between these pressures of selection and multifactorial characters such as head length, breadth, and height and characters of the facial morphology is therefore speculative. The variability of these characters is obviously only partly genetic in origin. The heritability of anthropological measurements of the face and the head is generally at a lower level than that of longitudinal body measurements (Susanne 1975, 1977). It is reasonable to think that the variability of these characters could be influenced a great deal by environmental factors such as differences in within-group (or between-group) demographic heterogeneity, differences in sample size (which influence total variability through differences in "random" variance), differences in the cultural homogeneity of the samples (between, for instance, a series of skeletons from the Neolithic period and a population from the 15th–18th century), and differences in population genetics such as variation in inbreeding as a function of increase in population size and variation in the mobility of individuals (and the possibility of genetic exchanges between populations).

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Prístup autorov k riešeniu stanovených otázok je seriózný, vychádza čiastočne z poznatkov ich starších prác. Prítom je dôkladne štatisticky podložený a zaujímavý z hľadiska zistených výsledkov.

Problematickým sa mi však zdá, že spolu s génovým posunom, inbreedingom a faktorom izolácie autori prakticky vylučujú z faktorov ovplyvňujúcich morfológickú variabilitu aj migráciu. Včasný stredovek je totiž obdobiím, kedy sa uskutočnili obrovské migračné pohyby európskeho obyvateľstva, najmä v dobe sťahovania národov. Vo včasnom stredoveku začal tiež príviv mongoloidných elementov do Európy (napr. Húni, Avari, starí Maďari etc.). Hoci sa podľa môjho skúmania (Thurzo 1976) zdá, že percento mongoloidných znakov na avarsko-slovanských a staromaďarských pohrebiskách je pomerne nízke (cca 15%, resp. 10%), ich pôsobenie na telesné charakteristiky obyvateľstva z územia mongoloidného vplyvu nemožno vylúčiť.

V práci sú použité náhodne vybrané vzorky publikovaných antropometrických údajov. Nepochybujem, že autori mali k dispozícii dostatočný počet údajov z rôznych oblastí Európy na uskutočnenie náhodného výberu. Je však otázne, či údaje z takto zvoleného jediného pohrebiska predstavujú reprezentatívnu populáciu pre určité obdobie a územie. Mnohé publikované údaje totiž pochádzajú z neúplne preskúmaných pohrebísk a tak nám charakterizujú iba väčšiu alebo menšiu časť pochovej populácie.

Uvádzanie nekorigovaných charakteristík živých individuí medzi údajmi z kostrového materiálu v tab. 3 dezorientuje čitateľa pri porovnávaní údajov. Podľa môjho názoru by bolo vhodné uviesť v tabulkách okrem označenia série a celkového počtu sérií aj celkové počty prípadov v sériách. Počet sérií s údajmi súčasných populácií sa mi zdá malý v porovnaní s údajmi geologicky aj kultúrne najstaršej skupiny.

Napriek trochu jednostrannému zameraniu považujem predloženú prácu za hodnotný príspevok k poznávaniu príčin vzniku a udržiavania sa variability kraniálnych charakteristík európskych populácií.

[The authors' approach is serious and based in part on earlier work. At the same time, their work is thoroughly documented by statistics and is interesting for its findings.

It seems problematic, however, that along with genetic drift, inbreeding, and the factor of isolation the authors for all practical purposes exclude migration from the factors influencing morphological variability. The early Middle Ages is a period in which vast migrations of the European population took place. In this period also began the influx of Mongoloid elements into Europe (e.g., Huns, Avars, ancient Magyars, etc.). Although according to my research (Thurzo 1976) it appears that the percentage of Mongoloid features in Avar-Slav and ancient Magyar burial grounds is comparatively low (ca. 10–15%), their influence on the physical characteristics of the population in the areas of Mongoloid influence cannot be excluded.

The work employs random samples of anthropometric data. I do not doubt that the authors had at their disposal sufficient data from various regions of Europe to lend themselves to random selection. It can be asked, however, whether data from a single burial ground so chosen are representative of the population for a given period and region. Many published data come from cemeteries that were not completely investigated, and as a result they characterize only a portion of the population.

The inclusion of uncorrected characterizations of living individuals among the data from skeletal material in table 3 only confuses the reader attempting to compare the data. In my view, it would have been fitting to include in the tables, in addition to the series and the total number of series, the total number of cases in a series. The number of series with data pertaining to contemporary populations seems small in comparison

with the number with data pertaining to the group that is geologically and culturally the oldest.

In spite of its somewhat one-sided orientation, I consider the work a valuable contribution to our knowledge of the causes of the origin and perpetuation of the variability of cranial characteristics of European populations.]

by ANDRZEJ WIERCIŃSKI

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This paper presents a first brilliant attempt at determining the role of natural selection in the development of inter- and intrapopulation variability over a large area of Europe during a time span of several millennia. It is a distinct example of a shift from more or less purely speculative theorizing to theorizing based on empirical evidence. Being in general agreement with the conclusions of the authors as to the role of natural selection and accepting their statistical findings, I would, however, like to raise the following issues for further discussion:

1. The estimation of the share of the component of selection in the process of increasing intragroup variability might provide a coefficient of correlation between I_{bs} and $m_{(s)}$; however, such a coefficient is absent, while figure 3 demonstrates less than moderate dependence.

2. It seems to me that the regular decrease of intergroup variability, measured by R_s and fully concordant with the result obtained by Schwidetzky (1972) for time series of averaged Penrose distance, is due more to the increase of gene exchange as a result of interbreeding between populations than to a slackening of selective pressure; in fact, the action of the latter component in this respect has not been demonstrated here.

3. I entirely disagree with the statement that the typological approach (applied to either populations or individuals) is necessarily based on the assumption that evolutionary factors, and especially natural selection, do not act upon contemporary man; on the contrary, it has been clearly shown, for instance (Wierciński 1971), that in Poland during the last millennium a very regular change in racial compositions occurred which can be reasonably explained only in terms of natural selection; in fact, it is only in the case of Czekanowski's concept that the stability of racial elements must be assumed, because of his quite arbitrary hypothesis that racial elements are inherited as monogenic traits would be.

I must strongly emphasize again that typology of populations or individuals is formally nothing more than a multivariate nominal measurement which aims to conceive the variability in terms of a set of racially diagnostic traits. The explanation of typologically observed differences or similarities between various human groups is quite another problem. These may be interpreted as resulting from convergent or divergent microevolution or from the interbreeding process responsible for interpopulational exchange of genes.

Reply

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In presenting our paper, we intended not only to offer some empirical results related to microevolutionary processes, but also, if not mainly, to spark discussion on methodological questions of the investigation of human variability and its causes. Unfortunately, the commentators have limited themselves to the repetition of well-known textbook statements about factors of evolution and their mode of operation and to consideration of particular problems related to our empirical basis. They

criticize our interpretation as being limited to the phenomenon of natural selection (this is because of a misunderstanding of our methodological stance, which we will discuss below) but are unable to cite empirical evidence for a quantitative relation between the operation of other evolutionary forces and the morphological changes observed in materials of the kind we have studied. In such a situation, it is worthwhile to devote some time to our methodological approach.

When we are considering a phenomenon known to be caused by a multitude of factors, including some that we not only cannot measure precisely, but cannot even define clearly, the only solution is to find out to what extent the factors we can define unequivocally and measure in a quantitative way influence the phenomenon in question. Obviously, in some cases the results of such an investigation will be unsatisfactory, i.e., the factors observed will not be significantly related to the phenomenon studied. Although it may sound trivial, we would like to repeat that in the history of any scientific discipline the stage of qualitative description is followed by the stage of quantitative modelling. Under the conditions just described—i.e., when one is able to observe quantitatively only some of the many factors involved—an idealizing scheme of investigation proves fruitful. Within this scheme, a working hypothesis is constructed as follows: on the basis of one's research experience, one assumes intuitively that one of the factors is of the greatest significance for the phenomenon in question and that other factors operate in such a manner that they do not substantially influence the relationship between this presumably main factor and the phenomenon. If the hypothesis is corroborated, i.e., if the factor chosen actually influences the phenomenon significantly, it is legitimate, irrespective of the strength of relationship discovered, to consider it as important and give it a high position in the hierarchy of essentiality. Formally, this main factor need not be responsible for the major portion of the variability in the phenomenon; it suffices to establish that no other single factor can explain more of the variability than the main one. Determination of the main factor in this way enables one to consider the corroborated hypothesis as a forceful theorem at a given stage of development of the scientific discipline. When no significant relationship between the phenomenon and the presumably main factor is revealed, the hypothesis must be rejected and another factor sought.

Our choice of natural selection as the main factor in microevolution did not result solely from the fact that of all the evolutionary forces it was the only one we knew how to approach quantitatively (by measuring the opportunity for it). We decided to "ignore" other factors after considering their relevance; we pointed this out in our paper, but apparently not strongly enough not to be overlooked by some of the commentators.

Most of the criticism is directed toward our view of migration (*sensu lato*); objections are variously formulated as breakdown of isolates, changing mobility, gene flow, decreasing inbreeding, and mass migrations (even the Crusades of the Middle Ages are mentioned). From the viewpoint of population biology, the relevance of these various aspects of mating systems varies, for the structure of populations may be considered jointly by observing the extent of deviation from the ideal state of fully random mating (and relatedly infinite population size) as assumed under Hardy-Weinberg conditions. We will here adopt the term "migration" to denote all these aspects. As we emphasized, migration in Europe within the period under consideration was, in our opinion, changing, but the sizes of breeding populations were such as to offer little probability of the operation of nondirectional forces of evolution related to effective population size. From archeological evidence it appears that in the agricultural regions of prehistoric Europe from the Neolithic on, population density was two or more persons per square kilometer (e.g., Angel 1972, Kurnatowski 1971) and permanent contacts were maintained within a radius of at least a dozen kilometers. Hence the effective population size of pre-

historic agriculturalists was very rarely less than 500. With such an effective population size, the effects of deviations from random mating can be considered negligible (Wright 1969).

Gene flow decreasing interpopulational differences (i.e., mobility of groups or individuals), which we also considered, is in accordance with Kelso's Law of Biocultural Evolution (cited by Beals) because of the level of adaptation (cultural as well as biological) of human groups. As we have pointed out, this general level of adaptation is measured by I_{bs} . Therefore, when we state that with the increasing adaptation of human groups (measured by I_{bs}) morphological characteristics change with respect to dispersion and central values, we may legitimately conclude that these changes result from the direct as well as indirect effects of *changing adaptation*. This latter phenomenon is under the control of natural selection whether the variability is of biological or of cultural origin.

The biological-state index is, of course, as we have said, a measure of the opportunity of reproductive success. Thus it determines the upper limit of adaptive possibilities for a given group. We do not intend to consider here the interpretative properties of I_{bs} , for we have done so elsewhere. Summing up, we would like to stress that, though they do not measure intensity of selection in a direct way, changes of I_{bs} values are approximately proportional to changes in selection intensity.

Some of the commentators (Huizinga et al., Salzano, Susanne) have touched on the question of the contribution of differential fertility to overall selection intensity. In relation to this we would like to say that—as is stated in our paper and illustrated by the formula for I_{bs} —the index takes into account a part of fertility in the form of the shape of the fertility function described by the set of s_x coefficients. Only the general intensity of producing offspring—total fertility rate—is not included in the index, and it is almost impossible to infer this rate directly from skeletal material. Furthermore, the portion of total phenotypic variance in fertility useful for selection is rather small, as is evidenced by heritability estimates (Fisher 1930, Henneberg 1978). Some indirect evidence given in Jacquard (1974) supports this conclusion. Low heritability estimates for fertility have also been obtained for other mammalian species (Falconer 1960). In our opinion, the relation between fertility and mortality is such that the entirety of reproduction may be described by either one, with the second being treated as the reverse of the first. It suffices to point to Salzano's obvious example of abortions. As he says, genetically determined abortions are a possible source of selection-relevant fertility differentials; but abortions are often called intrauterine *mortality* and may be formally treated as a mortality component in considerations of opportunity for selection (J. F. Crow, as quoted in Johnston and Kensinger 1971). The ultimate determination of the operation of natural selection is effectuated by reproduction as a whole (best measured by net reproductive rate or its derivative, the Malthusian parameter). The biological-state index measures jointly the effects of the majority of reproductive phenomena, ignoring only the total fertility rate. It is the direct measure of the average fitness of a group, for when the mean number of offspring produced by a pair of individuals is $2n$, size of a given generation (N_g) determines size of the next generation (N_{g+1}) in the following way:

$$N_{g+1} = nI_{bs}N_g,$$

hence $R_o = nI_{bs}$ (R_o being net reproductive rate). In this formula, I_{bs} replaces average fitness (\bar{w}) as used in the respective formulas in Chapter 10 of Jacquard's (1974) book.

Repeatedly the commentators (Huizinga et al., Rothhammer) raise objections to our choice of time scale. It is well established that various human populational measures show curvilinear correlations with calendar time. In particular, such

a type of relation is present in the case of I_{bs} values. The units of time we have employed were obtained from a transformation of the calendar time scale that gave us a straight regression line of I_{bs} with time. Since I_{bs} measures a considerable part of the average level of adaptation, we feel that it is legitimate to conclude that our units of cultural change correspond well to improvements of those elements of cultural systems that determine the adaptive abilities of human groups. When one considers the separate effects of technological advances (e.g., the production and use of metals) rather than the entirety of the adaptive efficiency of cultural systems, it may seem that we have wrongly defined our units of time. The observation of separate cultural details, independently of their number, to establish units of cultural change may understandably be misleading, for cultural systems are so complicated that the only reasonable way to obtain reliable estimates of their efficiency is to use synthetic measures. The names we have used for the cultural time units are conventional, traditionally rooted in archeology, and have, for most readers with some experience in European prehistory, intuitive meanings. There is no room here to describe all the differences between, e.g., Neolithic and Bronze Age human populations; it suffices to say that the differences are not confined to technology, but are equally clear in various aspects of organization, including ideology, art, etc. The archeological literature in this respect is abundant.

Some doubts are raised by commentators (Cook, Wierciński) as to the correlation between $m_{(s)}$ and I_{bs} . The relation of both measures to cultural time is presented in figure 3, but we have not presented the direct relation between them because—as we explained—each regression line is constructed using data pertaining to a different collection of skeletal samples. Despite this, it seems appropriate to calculate a correlation coefficient for mean values of $m_{(s)}$ and I_{bs} in these periods. When a given period is treated as the unit of observation, we may consider mean values of $m_{(s)}$ and I_{bs} as characteristics of the unit estimated on random samples. Then the correlation between I_{bs} and $m_{(s)}$ for the five periods we have used as units of time is linear and very high: $r = 0.97$, $t^2 = 6.49 > t_{0.01, 3} = 5.84$. This correlation underlies our conclusion concerning the importance of selection for changes in morphological variability within groups. If it were spurious, a third factor very strongly related to the two observed would have to be sought. In this situation no such search is necessary, since variance in I_{bs} explains more than 90% of the variance in $m_{(s)}$. While we are discussing problems of correlations, it is worthwhile to turn to the correlation of separate $m_{(s)}$ values with cultural time (fig. 2). Rothhammer reproaches us that this relation is not in fact as strong as we have seen it. There is no doubt that the correlation is linear and significant. Demonstration of the significance of a relation is usually sufficient proof of its existence. We would scarcely expect high covariance relative to overall variance estimated on samples where many sources of random error are present.

Many commentators question the choice of material and its quality. From the list of series given in our paper (table 1) it may be seen that we have utilized an average sample of data obtainable from publications on skeletal materials. The main criteria for choice of series are given in the paper, while details (archeological descriptions of sites and the like) are included in the published sources indicated. We do not feel obliged to reproduce from these publications all the information that a particular reader of our paper might be interested in. Obviously, we were unable to include in our sample every series published. Everyone who has worked with the published material on skeletal samples knows how diverse forms of data presentation are with respect to sets of characters considered, degree of statistical elaboration, etc. For such reasons, it is impossible to consider, for instance, the proposal of Huizinga et al. that we use Ukrainian materials; there are virtually no data on prehistoric mortality pertaining to this vast territory. Commentators have also wondered whether the characters observed are

good enough indicators of variability in their hereditary determinants. These doubts stem from the view that the heritability of metric characters is not high. We do not want to become involved here in a lengthy discussion on the problems of method bearing on the reliability of heritability estimates in human material—most of the estimates show that more than half of the phenotypic variance of the characters in question is due to genetic variability (more exactly, variance of additive effects), so that it is reasonable to expect that changes in the genotypic structure of populations will be reflected in their phenotypic variance. Consequently, if ecosensitivity is not related to genetic variability, these changes will also be reflected in heritability estimates because of certain properties of their definition; that is, measures of heritability are not direct estimates of the degree to which genetic endowment determines a character, but merely measures of the hereditarily determined portion of phenotypic variance in a certain situation limited in time and space.

The explanations given here are merely an expansion of what we have said in the paper. We have felt forced by the contents of the comments to adopt this form of reply, for the commentators, while raising a multitude of doubts as to the details of our work, have not formulated a coherent, empirically testable counterproposition. Nevertheless, we are grateful for so much interest in the problems we have touched on and consider the criticism stimulating for further investigations.

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