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Pilot Research Seeking Causative Factors for Morphological Characters: Ecological Correlations Between Morphological Characters, Genes of Biochemical/Physiological Characters, and Environmental Factors in Modern Humans

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Abstract As a step toward elucidating the causative factors of morphological characters, ecological correlations were estimated between specific morphological characters, the gene frequencies for biochemical/physiological characters, and environmental factors. Principal component analyses of the ecological correlations or the rotation of their results showed that the cephalic index had significant inverse associations with phosphoglucomutase 1, average annual temperature, and the amount of annual rainfall; that the nasal index had an inverse association with glyoxalase I and, simultaneously, positive associations with average annual temperature and the amount of annual rainfall; that the mesiodistal crown diameter of the maxillary first molar had significant associations with haptoglobin-alpha and average temperature in the coldest month; and that the buccolingual crown diameter of the maxillary second molar had an inverse association with alleles MS of the MNS system and, simultaneously, positive associations with average annual temperature and the amount of annual rainfall. These findings suggest that a morphological character comprises a character complex together with some biochemical/physiological characters which support the emergence or existence of the morphological character in a certain environment, or, merely, that an ecological association between a morphological character and a biochemical/physiological character is due to two independent adaptations to the same environmental factor or due to gene flow.
Key words: Morphological character, Protein, Gene, Principal component analysis, Bootstrap method

How is the form of our head, face or body determined? We know, to some extent, how genes and ontogenetic processes influence such structures. Recent post-genome researches are now identifying many genes for various characters including morphological ones (e.g., Dorus *et al.*, 2004). But the question remains: how and when those genes appeared and were fixed in our ancestral populations? It is impossible to determine the causes and mechanisms of their appearance by exploring only the genes of the human body. In order to attain this understanding, we must collect data on ancient environments in which morphological characters (namely, their genes) were brought into existence. At present, however, we do not have sufficient paleoecological data. We have, therefore, used data on environments inhabited by modern humans instead to search for the causes for the appearance of morphological characters, though indirectly.

As a result, some characters such as the cephalic index (Beals, 1972; Mizoguchi, 1985; Kouchi, 1986), nasal index (Yamaguchi, 1970; Carey and Steegmann, 1981; Mizoguchi, 1985), tooth crown size (Mizoguchi, 1993b), incisor shoveling (Mizoguchi, 1985) and Carabelli trait (Mizoguchi, 1993a) have demonstrated an association with environmental variables such as climatic factors, foodstuff intakes and/or ways of life. Although a few anthropologists like Scott

and Turner (1997) regard the geographical variations in frequencies of morphological dental characters as generated mainly through the processes of random genetic drift, many morphological characters have, in general, been accepted to have formed through adaptations to the environment.

On the other hand, it is widely known that some genes for biochemical characters, such as the ABO blood-group system, the Rhesus system, hemoglobin S, beta-thalassemia, glucose-6-phosphate dehydrogenase, alpha-2HS-glycoprotein, etc., show geographical clines in their frequencies or have ecological correlations with latitude and/or climatic factors (Piazza *et al.*, 1981; O'Rourke *et al.*, 1985; Cavalli-Sforza and Cavalli-Sforza, 1995; Lewontin, 1995; Spitsyn *et al.*, 1998; Ciminelli *et al.*, 2000). Some of these clines or correlations have been interpreted as the result of gene flow or migration, and the causes of others have been explained by adaptations to various environments through selection.

Further, there is a study by Relethford (2004) which comprehensively examined the contribution of isolation by geographic distance to the present global variation patterns in three kinds of characters, i.e., red blood cell polymorphisms, microsatellite DNA markers, and craniofacial measurements. In his paper, Relethford maintains that, since a common pattern of global gene flow mediated by geographic distance is detectable in diverse genetic and morphological data sets, the correspondence between genetic similarity and geographic distance may reflect the history of dispersal of the human species out of Africa.

In this preliminary study, the present author attempts to examine how a morphological character is associated with natural or cultural environmental factors along with biochemical/physiological characters by analyzing all these data types simultaneously. In other words, this study examines the possibility that some biochemical/physiological characters support the existence of a morphological character in a certain environment.

Over ten years ago, the present author (Mizoguchi, 1994) conducted a similar study. At that time, he examined ecological correlations (Yasuda, 1969), i.e., among-group correlations between ten morphological characters, ten alleles for biochemical/physiological characters, and ten environmental variables, and found that as many as eight of the ten alleles for biochemical/physiological characters showed significant ecological correlations with morphological characters, suggesting the existence of some character complexes composed of both morphological and biochemical/physiological characters. In the present study, many more, i.e., 37 alleles for biochemical/physiological characters are examined to investigate the biochemical/physiological background of morphological characters in more depth.

Materials and Methods

All the data used were collected from the literature (Table 1). Morphological data are the mean values or frequencies of somatometric and dental characters compiled by Mizoguchi (1985, 1993a), and biochemical/physiological data are the frequencies of 37 alleles of various polymorphic genes for enzymes, proteins, blood groups, etc. published by Roychoudhury and Nei (1988). Environmental variables are climatic and cultural ones, the latter of which are the way of life variables from the 15th century, and were compiled by Mizoguchi (1985). Using these data, 21 pooled samples were created for the present analysis.

The analysis has three steps. In the first step, those alleles for biochemical/physiological characters which were significantly correlated with a morphological character were screened using Kendall's rank correlation coefficient, tau (Siegel, 1956).

In the second step, a set comprised of a morphological character and all the related biochemical/physiological characters was examined by principal component analysis (Lawley and Maxwell, 1963; Okuno *et al.*, 1971, 1976; Takeuchi and Yanai, 1972; abbreviated as PCA

Table 1. Means or frequencies of morphological characters, environmental variables and polymorphic genes in modern human pozpulations worldwide.[a]

Population	Stature (cm)[b]	Cephalic index[b]	Nasal index[b]	MD diam. of UI1 (mm)[c]	MD diam. of UM1 (mm)[c]	MD diam. of UM2 (mm)[c]
Mongolian	166	85				
Chinese	165	80	71	8.60	10.30	9.90
Native Taiwanese	161	79	94	8.50	10.50	9.90
Korean	165	85	72	8.70	10.20	9.80
Ainu	160	77	78	8.29	10.19	9.23
Japanese	161	81	77	8.74	10.66	9.81
Bhutanese	158	77	75	8.42[d]	10.07[d]	8.87[d]
Jat	164	74	63	8.78	10.76	9.83
Afghan	166	86	65	8.34	9.94	8.92
Arab	166	77	65	8.76	10.63	10.03
Melanesian	165	77	94	9.00	11.12	10.31
Native Australian	167	74	108	9.36	11.20	10.83
Polynesian	171	81	76	8.72	10.68	10.09
Inuit	163	82	68	8.70	11.10	10.40
Native U.S. American	169	80	85	9.14	11.03	10.46
Native Mexican	155	84		8.55	10.34	
Native S. American	163	82		9.10	11.28	10.85
Northern Russian	159	83				
Lapp	156	86	69	8.79	10.53	9.87
European	169	83	67	8.77	10.54	10.04
African	167	76	102	9.31	11.24	10.95
Median	165	81	75	8.74	10.63	9.965

[a] Each of the 21 groups listed here was created by pooling several samples which were supposedly derived from a certain population. Each listed value is the median among the frequencies or means for one or more samples from the population. [b] Male data (Mizoguchi, 1985). [c] Male data (Mizoguchi, 1993a). [d] Prakash *et al.* (1979).

Table 1. (Continued—2)

Population	BL diam. of UM1 (mm)[c]	BL diam. of UM2 (mm)[c]	Shoveling (%)[e]	Carabelli trait (%)[f]	Latitude (°)[g]	Average annual temp. (°C)[g]
Mongolian			100	14	48 N	−3.1
Chinese	11.50	11.70	92	9	31 N	13.6
Native Taiwanese	11.70	11.60	98	37	24 N	23.5
Korean	11.60	11.80	84	25	38 N	12.1
Ainu	11.30	11.10	83	9	43 N	7.1
Japanese	11.92	11.56	94	29	36 N	14.2
Bhutanese	11.16[d]	11.11[d]			28 N	23.3
Jat	11.21	10.69	87	36	30 N	25.3
Afghan	11.14	11.26		34	33 N	15.0
Arab	11.54	11.55	33	65	32 N	17.7
Melanesian	12.10	12.35	73	18	6 S	26.3
Native Australian	12.55	12.77	68		24 S	20.7
Polynesian	11.95	12.22	82	34	20 S	26.7
Inuit	11.80	11.80	100	63	69 N	−4.0
Native U.S. American			98	17	36 N	15.5
Native Mexican	11.40			66	23 N	21.7
Native S. American	11.76	11.41	98	14	25 S	23.4
Northern Russian				26	68 N	0.2
Lapp	11.73	11.66	44	28	68 N	2.4
European	11.32	11.28	34	40	54 N	7.1
African	11.80	11.90	34	34	5 S	25.5
Median	11.65	11.60	84	29	32[h]	15.5

[e] All affected expressivities of UI1 shoveling (Mizoguchi, 1985). Males and females are combined.
[f] Strongest expressivities (grades 2+3) in the UM1 (Mizoguchi, 1993a). Males and females are combined.
[g] Mizoguchi (1985). The climatic measurements for each group were approximately estimated based on data from several meteorological stations near the localities from which the samples were derived.
[h] Median of the absolute values regardless of whether data were from the Northern or Southern Hemisphere.

Table 1. (Continued—3)

Population	Av. temp. in the hottest month (°C)[g]	Av. Temp. in the coldest month (°C)[g]	Mean relative annual humidity (%)[g]	Amount of annual rainfall (mm)[g]	Hunting-gathering[i]	Cattle breeding[i]
Mongolian	16.1	−25.6	65	208	0	1
Chinese	28.0	−2.8	60	677	0	1
Native Taiwanese	28.1	17.9	80	2281	0	1
Korean	25.1	−1.0	69	1126	0	1
Ainu	20.0	−5.5	78	1212	1	0
Japanese	25.7	2.6	72	1210	0	0
Bhutanese	28.1	15.2	77	1582	0	1
Jat	34.5	14.3	49	715	0	1
Afghan	26.8	1.8	50	258	0	1
Arab	26.6	8.0	51	254	0	1
Melanesian	26.8	24.8	82	2055	0	1
Native Australian	28.2	15.0	59	523	1	0
Polynesian	27.6	26.0	78	2224	0	1
Inuit	6.9	−19.9	82	236	1	0
Native U.S. American	23.9	6.5	48	309	1	0
Native Mexican	27.2	14.2	66	726	0	0
Native S. American	25.8	17.0	76	1531	0	1
Northern Russian	14.1	−11.7	80	464	0	1
Lapp	13.5	−6.9	78	713	0	1
European	17.1	−2.2	83	594	0	1
African	26.1	24.4	80	1625	1	1
Median	26.1	6.5	76	715		

[i] Ways of life in the 15th century (Ishige, 1973; Mizoguchi, 1985). 1=Adoption; 0=No adoption.

Table 1 (Continued—4)

Population	Milking[i]	Agri-culture[i]	Enzymes[j]			
			ACP1*a	ACP1*b	ADA*1	AK1*1
Mongolian	1	0	.227	.773	.953	.984
Chinese	0	1	.214	.786	.939	1.000
Native Taiwanese	0	1			.935	1.000
Korean	0	1	.220	.780	.947	.967
Ainu	0	0	.274	.726	.972	1.000
Japanese	0	1	.210	.790	.969	1.000
Bhutanese	1	1	.171	.829		1.000
Jat	1	1				
Afghan	1	1	.297	.683	.866	.920
Arab	1	1	.181	.810	.862	.975
Melanesian	0	1	.205	.795	.847	1.000
Native Australian	0	0	.010	.990	.995	1.000
Polynesian	0	1	.214	.786	.890	1.000
Inuit	0	0	.601	.399	1.000	.992
Native U.S. American	0	0				
Native Mexican	0	1	.175	.825		
Native S. American	0	1	.061	.939	1.000	1.000
Northern Russian	0	0	.190	.794		.998
Lapp	0	0	.488	.493	.863	.993
European	1	1	.356	.588	.944	.964
African	1	1	.133	.849	.996	.994
Median			.212	.788	.9455	.999

[j] Roychoudhury and Nei (1988). ACP1*a=allele a of acid phosphatase 1; ACP1*b=allele b of acid phosphatase 1; ADA*1=allele 1 of adenosine deaminase; AK1*1=allele 1 of soluble adenylate kinase 1;

Table 1. (Continued—5)

Population	Enzymes[j]					
	CHE1*u	CHE2*−	ESD*1 [=FGH*1]	G6PD*B+	GPT1*1, AAT1*1	GLO1*1
Mongolian			.699		.614	.227
Chinese	.998		.637	.976	.500	.200
Native Taiwanese			.683			.193
Korean	1.000	.989	.676	.986	.602	.116
Ainu	1.000	.971	.681	1.000	.455	
Japanese	.997	.957	.600	.999	.623	.088
Bhutanese		.946		1.000		
Jat					.529	
Afghan	1.000		.897	.975	.455	
Arab	.991			.873		
Melanesian		.997	.934	.989	.733	.043
Native Australian	1.000	1.000	.968	1.000	.809	.000
Polynesian		1.000	.611	.982	.547	.233
Inuit	1.000	.944	.822	1.000	.609	.360
Native U.S. American	1.000					
Native Mexican	.989					
Native S. American	.984	.971	.687	1.000	.388	.213
Northern Russian						
Lapp	.984	.946	.907		.611	.304
European	.984	.950	.908	1.000	.536	.439
African	.937		.972	.755	.873	.259
Median	.9975	.971	.699	.994	.602	.213

CHE1*u=allele u of cholinesterase [serum] 1, pseudocholinesterase 1; CHE2*−=allele – of cholinesterase 2, pseudocholinesterase 2; ESD*1 [=FGH*1]=allele 1 of esterase D [= S-formylglutathione hydrolase]; G6PD*B+=allele B+ of glucose-6-phosphate dehydrogenase; GPT1*1, AAT1*1=allele 1 of glutamic-pyruvate transaminase, alanine aminotransferase; GLO1*1=alelle 1 of glyoxalase I;

Table 1. (Continued—6)

Population	Enzymes[j]		Proteins[k]			
	PGM1*1	PGD*A	GC, DBP*1	HPA*1	HBB*A	BF, GBG*S
Mongolian		.872	.765	.270		
Chinese	.732	.933	.756	.275	.997	.885
Native Taiwanese	.934		.828	.256		.885
Korean	.775	.893	.696	.279		.723
Ainu	.870	.928	.777	.113		
Japanese	.766	.910	.756	.266	1.000	.824
Bhutanese	.770	.770		.130	.981	
Jat						
Afghan	.733	.954	.769	.271		.696
Arab	.742	.926		.345	.989	.517
Melanesian	.934	.864	.576	.684	1.000	.894
Native Australian	.909	.950	.900	.207	1.000	
Polynesian	.669	.877	.753	.552	1.000	.711
Inuit	.787	.998	.689	.332	1.000	.989
Native U.S. American			.819	.455		.973
Native Mexican	.784	1.000	.819	.548		
Native S. American	.829	1.000	.821	.580	1.000	.915
Northern Russian	.655	.957		.390		
Lapp	.550	.919	.823	.314	1.000	.888
European	.782	.980	.725	.381	1.000	.791
African	.849	.929	.766	.574	.9994	
Median	.7785	.9285	.766	.323	1.000	.885

PGM1*1=allele 1 of phosphoglucomutase 1; PGD*A=allele A of phosphogluconate dehydrogenase.

[k] Roychoudhury and Nei (1988). GC,DBP*1=allele 1 of group-specific component, vitamin D binding protein; HPA*1=allele 1 of haptoglobin, alpha; HBB*A=allele A of hemoglobin, beta; BF,GBG*S=allele S of properdin factor B, glycine-rich beta-glycoprotein;

Table 1. (Continued—7)

Population	Proteins[k]		Blood groups[l]			
	BF, GBG*F	TF*C	Se	B	O	Di*b
Mongolian		.983		.231	.567	
Chinese	.114	.945	.479	.171	.636	.957
Native Taiwanese	.115			.124	.692	1.000
Korean	.273	.988	.491	.213	.558	.953
Ainu		.990	.339	.199	.558	.976
Japanese	.176	.989	.510	.177	.548	.951
Bhutanese		.990		.190	.565	.976
Jat						
Afghan	.268	.994		.186	.582	
Arab	.321	.999		.127	.700	.985
Melanesian	.106	.973	.691	.100	.674	1.000
Native Australian		.885	.988	.000	.75	1.000
Polynesian	.283	1.000	.437	.130	.610	1.000
Inuit	.010	1.000	.942	.079	.648	.979
Native U.S. American	.015	.982	.779	.007	.708	.974
Native Mexican		.976		.004	.946	.944
Native S. American	.063	1.000	.907	.000	1.000	.824
Northern Russian				.230	.630	
Lapp	.112	.994	.736	.069	.499	1.000
European	.196	.993	.530	.080	.646	1.000
African		.976	.493	.091	.714	1.000
Median	.115	.9895	.530	.1255	.641	.979

BF, GBG*F=allele F of properdin factor B, glycine-rich beta-glycoprotein; TF*C=allele C of transferrin.
[l] Roychoudhury and Nei (1988). Se=allele Se of ABH secretion; B=allele B of ABO system; O=allele O of ABO system; Di*b=allele Di*b of Diego system;

Table 1. (Continued—8)

Population	Blood groups[l]					
	k	Jk*a	Le	Lu*b	MS	Ms
Mongolian	.996	.409			.055	.496
Chinese	.999	.349	.492	.996	.159	.531
Native Taiwanese	1.000		.414		.000	.500
Korean	.999	.466	1.000	1.000	.029	.493
Ainu	1.000		.684	1.000	.020	.393
Japanese	1.000	.472	.812	1.000	.064	.466
Bhutanese	1.000			1.000	.141	.545
Jat		.520		1.000		
Afghan	.982	.558		.975	.266	.370
Arab	.967			.994	.294	.374
Melanesian	1.000	.398	.133	1.000	.007	.097
Native Australian	1.000		.566	1.000	.000	.263
Polynesian	1.000			1.000	.013	.662
Inuit	1.000	.736	1.000	1.000	.183	.659
Native U.S. American	1.000		.400	1.000	.331	.463
Native Mexican	1.000			1.000	.376	.406
Native S. American	1.000	.407	.440	.999	.20	.541
Northern Russian	1.000				.081	.424
Lapp	.994	.577	.684	.978	.253	.203
European	.963	.511	.780	.962	.241	.329
African	.997	.859	.308	.975	.118	.353
Median	1.000	.4915	.566	1.000	.1295	.4435

k=allele k of Kell system; Jk*a=allele Jk*a of Kidd system; Le=allele Le of Lewis system; Lu*b=allele Lu*b of Lutheran system; MS=alleles MS of MNS system; Ms=alleles Ms of MNS system;

Table 1. (Continued—9)

Population	Blood groups[l]				
	Ns	P*1	cde	CDe	cDE
Mongolian	.438	.193			
Chinese	.440	.186	.036	.646	.230
Native Taiwanese	.437		.000	.882	.098
Korean	.472	.175	.026	.641	.214
Ainu	.355	.098	.024	.539	.268
Japanese	.444	.198	.033	.646	.262
Bhutanese	.280	.236	.039	.666	.289
Jat		.442			
Afghan	.275	.462	.283	.501	.160
Arab	.263	.515	.319	.405	.133
Melanesian	.770	.196	.000	.874	.077
Native Australian	.737	.148	.000	.65	.21
Polynesian	.325	.270	.000	.574	.327
Inuit	.158	.191	.000	.488	.468
Native U.S. American	.131	.457	.044	.596	.337
Native Mexican	.147	.367	.000	.602	.323
Native S. American	.130	.514	.000	.527	.367
Northern Russian	.487	.233	.068	.470	.462
Lapp	.363	.346	.195	.596	.179
European	.365	.531	.387	.418	.153
African	.372	.717	.168	.041	.043
Median	.364	.253	.033	.596	.230

Ns=alleles Ns of MNS system; P*1=allele P*1 of P system; cde=alleles cde of Rhesus system; CDe=alleles CDe of Rhesus system; cDE=alleles cDE of Rhesus system;

Table 1. (Continued—10)

Population	Miscellaneous[m]			
	Cerumen (W)	Color-blindness (CB)	Lactase activity (LAA)	PTC (T)
Mongolian	.062	7.2	12.1	.672
Chinese	.081	5.8	3.9	.774
Native Taiwanese	.465			
Korean	.076	5.1		.634
Ainu	.295	0.5		.754
Japanese	.085	4.4	15.2	.647
Bhutanese				
Jat				
Afghan	.608		17.4	
Arab			71.7	.396
Melanesian	.473	4.6	15.4	.636
Native Australian	.821	1.9	33.1	.298
Polynesian		7.5		.597
Inuit		2.5	12.0	.381
Native U.S. American	.227	1.1		.794
Native Mexican	.243	3.6		.654
Native S. American		2.3		.839
Northern Russian				
Lapp			58.4	.468
European	.642	8.2	90.0	.434
African		3.9	21.7	.847
Median	.269	4.15	17.4	.6415

[m] Roychoudhury and Nei (1988). Cerumen (W)=allele W for the wet type of ear wax; Colorblindness (CB)=percentage of colorblind males; Lactase activity (LAA)=percentage of lactose absorbers; PTC (T)=allele T for a taster of phenylthiocarbamide.

below) to ascertain the interrelationships among these variables in more detail. In this case, correlations between characters were evaluated by Pearson's product-moment correlation coefficient. The number of principal components (PCs) used was determined so that the cumulative proportion of the variances of the principal components exceeded 80%. The principal components obtained in such a way were then transformed by Kaiser's normal varimax rotation method (Asano, 1971; Okuno *et al.*, 1971) into different factors to reveal any other associations hidden behind the variables. Although it is not necessarily expected for the among-group distribution of a mean value or gene frequency to be normal, the statistical significance of a factor loading can be tested using the bootstrap method (Efron, 1979a, b, 1982; Diaconis and Efron, 1983; Mizoguchi, 1993b) because this method does not depend on the form of the distribution. For estimating the bootstrap standard deviation for factor loading, 1,000 bootstrap replications including the observed sample were used. The bootstrap standard deviation was estimated by directly counting the cumulative frequency of the standard deviation in the bootstrap distribution.

In the above PCA of the second-step analysis, the number of biochemical/physiological characters to be analyzed was determined according to the level of statistical significance for Kendall's tau in the first-step analysis so that the sample size was appropriate for the PCA under the statistical restriction on sample size given the number of variables. Further, if two or more alleles at the same locus or two or more genotypes for the same biochemical/physiological characters were correlated with a morphological character, only one of them was used for this PCA.

In the final step, a character complex composed of a morphological character and the strongly related biochemical/physiological characters was also examined by PCA and Kaiser's normal varimax rotation method to determine whether it was associated with any natural or cultural environmental factors. In this PCA, only those biochemical/physiological characters which were found to be significantly or most highly associated with a relevant morphological character in the second-step analysis were analyzed. In addition to these, however, the following two physiological characters were also analyzed because their adaptive significance is well known: color-blindness, which is considered to be associated with agriculture (Hoshi, 1977), and lactase activity, which still remains high in adults in Europe and a few other places where there is a history of rearing cattle (Jones, 1992). In order to evaluate correlations with 0–1 variables, the four-fold point correlation coefficient, which corresponds to the product-moment correlation coefficient formally calculated based on 0–1 data (Yasuda, 1969), was used.

The above statistical calculations were executed with the mainframe, HITACHI MP5800 System, at the Computer Centre, University of Tokyo. The programs used were RKCNCT for calculating rank correlation coefficients, and BTPCA for principal component analysis and Kaiser's normal varimax rotation. These programs were written in FORTRAN by the present author.

Results

Screening by rank correlation coefficient

First of all, biochemical/physiological characters having strong correlations with morphological characters were roughly analyzed using Kendall's rank correlation coefficient. As a result, 31 (83.8%) of 37 alleles for biochemical/physiological characters were found to have significant correlations with a subset of the ten morphological characters at the 5% level (Table 2).

Character complexes composed of morphological and biochemical/physiological characters

In the second step, principal component analysis was applied to each ecological correlation matrix on a set comprised of a morphological character and those biochemical/physiological characters which were found to be significantly correlated with the relevant morphological char-

Table 2. Ecological correlations of morphological characters with polymorphic genes for enzymes, proteins, blood groups, etc.[a]

Morphological character	–Allele for a biochemical/physiological character	No. of pairs	Kendall's tau
Stature	– Cholinesterase 2, pseudocholinesterase 2 (CHE2*−)	11	0.50*
	– Glucose-6-phosphate dehydrogenase (G6PD*B+)	14	−0.45*
	– Kell system (k)	20	−0.33*
Cephalic index	–Acid phosphatase 1 (ACP1*a)	18	0.46**
	–Acid phosphatase 1 (ACP1*b)	18	−0.48**
	– Soluble adenylate kinase 1 (AK1*1)	18	−0.44*
	– Phosphoglucomutase 1 (PGM1*1)	18	−0.42*
	– ABO system (O)	20	−0.35*
	– Lewis system (Le)	13	0.45*
	– Colorblindness (CB)	14	0.40*
Nasal index	– Acid phosphatase 1 (ACP1*a)	14	−0.49*
	– Acid phosphatase 1 (ACP1*b)	14	0.49*
	– Soluble adenylate kinase 1 (AK1*1)	15	0.60**
	– Cholinesterase 2, pseudocholinesterase 2 (CHE2*−)	10	0.57*
	– Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	13	0.50*
	– Glyoxalase I (GLO1*1)	11	−0.64**
	– Phosphoglucomutase 1 (PGM1*1)	15	0.44*
	– Transferrin (TF*C)	15	−0.52**
	– Kell system (k)	16	0.52**
	– Lewis system (Le)	12	−0.53*
	– MNS system (MS)	16	−0.60**
	– Rhesus system (cde)	16	−0.42*
	– Rhesus system (CDe)	16	0.39*
MD of UI1	– Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	14	0.47*
	– Haptoglobin, alpha (HPA*1)	18	0.44*
	– ABH secretion (Se)	13	0.54**
	– ABO system (B)	18	−0.51**
	– ABO system (O)	18	0.34*
MD of UM1	– Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	14	0.42*
	– Haptoglobin, alpha (HPA*1)	18	0.46**
	– Properdin factor B, glycine-rich beta-glycoprotein (BF,GBG*S)	13	0.43*
	– ABH secretion (Se)	13	0.46*
	– ABO system (B)	18	−0.47**
	– ABO system (O)	18	0.45**
MD of UM2	– Haptoglobin, alpha (HPA*1)	17	0.53**
	– Properdin factor B, glycine-rich beta-glycoprotein (BF, GBG*S)	13	0.45*
	– ABH secretion (Se)	13	0.46*
	– ABO system (B)	17	−0.66***
	– ABO system (O)	17	0.61***
	– Lewis system (Le)	13	−0.42*
BL of UM1	– Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1, AAT1*1)	14	0.58**
	– Hemoglobin, beta (HBB*A)	12	0.48*
	– MNS system (MS)	17	−0.44*
	– Rhesus system (cde)	17	−0.41*
BL of UM2	– Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1, AAT1*1)	14	0.49*
	– MNS system (MS)	16	−0.40*
	– MNS system (Ns)	16	0.37*
Shoveling	– Properdin factor B, glycine–rich beta–glycoprotein (BF,GBG*S)	12	0.58**
	– Properdin factor B, glycine-rich beta-glycoprotein (BF, GBG*F)	12	−0.56*
	– Diego system (Di*b)	15	−0.46*

Table 2. (Continued)

Morphological character–Allele for a biochemical/physiological character		No. of pairs	Kendall's tau
	– Kell system (k)	16	0.40*
	– Lutheran system (Lu*b)	15	0.44*
	– MNS system (Ms)	16	0.46*
	– Rhesus system (cde)	15	−0.38*
	– Rhesus system (cDE)	15	0.59**
	– Lactase activity (LAA)	10	−0.70**
Carabelli trait	– Kidd system (Jk*a)	12	0.62**
	– P system (P*1)	18	0.38*
	– PTC (T)	15	−0.45*

[a] Only significant rank correlation coefficients are listed.
* $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed test.

acter in the first-step examination. The direct results of the PCAs and their rotated solutions for stature, cephalic index, nasal index, the mesiodistal (MD) crown diameter of the maxillary central incisor (UI1), the MD diameters of the maxillary first molar (UM1) and the maxillary second molar (UM2), the buccolingual (BL) diameters of UM1 and UM2, shoveling of UI1, and Carabelli trait of UM1 are shown in Tables 3 to 18. Among these, significant associations can be found in Tables 6, 8, 9, 11, 12 and 16. They are as follows: an inverse association between the cephalic index and allele 1 of phosphoglucomutase 1 (Table 6); an inverse association between the nasal index and allele C of transferrin (Table 8); an inverse association between the MD diameter of UI1 and allele B of the ABO system (Table 9); positive associations between the MD diameters of UM1 and UM2 and allele 1 of haptoglobin-alpha, allele S of properdin factor B glycine-rich beta-glycoprotein, and allele Se of the ABH secretion, as well as an inverse association with allele B of the ABO system (Tables 11 and 12); and a positive association between shoveling and alleles cDE of the Rhesus system (Table 16).

Associations with natural or cultural environmental factors

For the final step, natural or cultural environmental factors that may have influenced a character complex composed of morphological and biochemical/physiological characters was probed. The direct results of the PCAs and their rotated solutions for such character complexes and climatic variables are shown in Tables 19 to 54, and those for the character complexes and the ways of life are shown in Tables 55 to 90.

The significant associations that were detected are as follows.

First, the cephalic index and phosphoglucomutase 1 constitute a character complex, and this complex is significantly associated with annual temperature and rainfall (Table 21). More exactly speaking, the first principal component (PC I) which is significantly correlated with the cephalic index is inversely correlated with allele 1 of phosphoglucomutase 1, average annual temperature, average temperature in the hottest month, average temperature in the coldest month, and the amount of annual rainfall. As for associations with cultural factors, however, no evidence supported that this character complex is significantly associated with any of the ways of life (Tables 57 and 58).

Colorblindness was significantly correlated with the cephalic index in the first-step analysis (Table 2). But, through the second (Tables 5 and 6) and final (Tables 23, 24, 59 and 60) steps, no significant tendency was found to support the association of these two characters as a character complex.

The nasal index, along with average annual temperature, average temperature in the hottest

Table 3. Principal component analysis of the ecological correlations on stature and allele frequencies for biochemical characters.[a]

Variable	Factor loadings		Total variance (%)
	PC I	II	
Stature	−0.76	−0.60	93.25
Cholinesterase 2, pseudocholinesterase 2 (CHE2*−)	−0.89	0.24	85.76
Glucose-6-phosphate dehydrogenase (G6PD*B+)	0.89	−0.11	79.70
Kell system (k)	−0.14	0.97	96.18
Total contribution (%)	54.58	34.14	88.72
Cumulative proportion (%)	54.58	88.72	88.72

[a] The number of populations used is 10. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 4. Solution obtained through the normal varimax rotation of the first two principal components (Table 3) from the ecological correlations on stature and allele frequencies for biochemical characters.[a]

Variable	Factor loadings	
	Fac I	II
Stature	−0.72	−0.65
Cholinesterase 2, pseudocholinesterase 2 (CHE2*−)	−0.91	0.18
Glucose-6-phosphate dehydrogenase (G6PD*B+)	0.89	−0.05
Kell system (k)	−0.21	0.96

[a] The cumulative proportion of the two principal components is 88.72%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 5. Principal component analysis of the ecological correlations on cephalic index and allele frequencies for biochemical characters.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Cephalic index	−0.85	0.22	0.38	91.77
Acid phosphatase 1 (ACP1*a)	−0.66	−0.49	−0.02	67.24
Soluble adenylate kinase 1 (AK1*1)	0.77	−0.33	0.18	72.92
Phosphoglucomutase 1 (PGM1*1)	0.80	−0.10	−0.26	71.66
ABO system (O)	0.51	0.50	0.63	91.26
Lewis system (Le)	−0.79	−0.42	0.25	86.16
Colorblindness (CB)	−0.59	0.64	−0.42	93.95
Total contribution (%)	51.78	17.68	12.68	82.14
Cumulative proportion (%)	51.78	69.46	82.14	82.14

[a] The number of populations used is 10. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 6. Solution obtained through the normal varimax rotation of the first three principal components (Table 5) from the ecological correlations on cephalic index and allele frequencies for biochemical characters.[a]

Variable	Factor loadings		
	Fac I	II	III
Cephalic index	−0.42	0.04	0.86*
Acid phosphatase 1 (ACP1*a)	0.01	−0.61	0.55
Soluble adenylate kinase 1 (AK1*1)	0.71	0.20	−0.42
Phosphoglucomutase 1 (PGM1*1)	0.36	0.10	−0.76*
ABO system (O)	0.20	0.93	−0.04
Lewis system (Le)	0.01	−0.45	0.81†
Colorblindness (CB)	−0.96*	−0.07	0.10

[a] The cumulative proportion of the three principal components is 82.14%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 7. Principal component analysis of the ecological correlations on nasal index and allele frequencies for biochemical characters.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Nasal index	−0.78	−0.41	0.16	80.49
Soluble adenylate kinase 1 (AK1*1)	−0.68	0.46	0.52	94.29
Glyoxalase I (GLO1*1)	0.91	0.06	0.29	90.68
Transferrin (TF*C)	0.68	0.56	−0.32	87.86
Kell system (k)	−0.75	0.59†	−0.02	90.49
MNS system (MS)	0.82	−0.00	0.52	93.94
Total contribution (%)	59.71	17.41	12.50	89.62
Cumulative proportion (%)	59.71	77.13	89.62	89.62

[a] The number of populations used is 10. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 8. Solution obtained through the normal varimax rotation of the first three principal components (Table 7) from the ecological correlations on nasal index and allele frequencies for biochemical characters.[a]

Variable	Factor loadings		
	Fac I	II	III
Nasal index	−0.80*	0.19	−0.36
Soluble adenylate kinase 1 (AK1*1)	−0.28	0.93†	−0.08
Glyoxalase I (GLO1*1)	0.43	−0.28	0.80†
Transferrin (TF*C)	0.92***	−0.11	0.16
Kell system (k)	0.00	0.78	−0.54
MNS system (MS)	0.24	−0.16	0.93†

[a] The cumulative proportion of the three principal components is 89.62%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 9. Principal component analysis of the ecological correlations on the MD diameter of UI1 and allele frequencies for biochemical characters.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UI1	−0.93***	0.22	−0.08	92.52
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	−0.57	0.64	−0.49	97.52
Haptoglobin, alpha (HPA*1)	−0.53	0.37	0.75†	98.22
ABH secretion (Se)	−0.77	−0.55	−0.15	92.31
ABO system (B)	0.89**	0.38	−0.08	93.80
Total contribution (%)	56.97	21.07	16.84	94.88
Cumulative proportion (%)	56.97	78.03	94.88	94.88

[a] The number of populations used is 12. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.

† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 10. Solution obtained through the normal varimax rotation of the first three principal components (Table 9) from the ecological correlations on the MD diameter of UI1 and allele frequencies for biochemical characters.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UI1	−0.58	0.66†	0.39
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	−0.07	0.98*	0.05
Haptoglobin, alpha (HPA*1)	−0.11	0.11	0.98†
ABH secretion (Se)	−0.96†	0.10	−0.03
ABO system (B)	0.92*	−0.14	−0.27

[a] The cumulative proportion of the three principal components is 94.88%.

† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 11. Principal component analysis of the ecological correlations on the MD diameters of UM1 and UM2 and allele frequencies for biochemical characters.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UM1	0.94***	−0.06	0.18	91.53
MD of UM2	0.94***	0.12	−0.16	92.87
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	−0.24	−0.61	0.74†	97.49
Haptoglobin, alpha (HPA*1)	0.77*	−0.57	−0.18	94.72
Properdin factor B, glycine-rich beta-glycoprotein (BF,GBG*S)	0.76***	0.18	0.39	76.37
ABH secretion (Se)	0.87***	0.33	0.31	95.89
ABO system (B)	−0.88**	−0.21	0.12	82.56
Lewis system (Le)	−0.52	0.71	0.33	87.78
Total contribution (%)	59.83	17.46	12.60	89.90
Cumulative proportion (%)	59.83	77.30	89.90	89.90

[a] The number of populations used is 8. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.

† $p<0.10$;* $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 12. Solution obtained through the normal varimax rotation of the first three principal components (Table 11) from the ecological correlations on the MD diameters of UM1 and UM2 and allele frequencies for biochemical characters.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UM1	0.85*	−0.44	−0.01
MD of UM2	0.76*	−0.44	−0.39
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	−0.08	−0.06	0.98*
Haptoglobin, alpha (HPA*1)	0.39	−0.89	0.01
Properdin factor B, glycine-rich beta-glycoprotein (BF,GBG*S)	0.87	−0.08	0.06
ABH secretion (Se)	0.97*	−0.05	−0.10
ABO system (B)	−0.76†	0.32	0.39
Lewis system (Le)	−0.07	0.93	−0.02

[a] The cumulative proportion of the three principal components is 89.90%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 13. Principal component analysis of the ecological correlations on the BL diameters of UM1 and UM2 and allele frequencies for biochemical characters.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
BL of UM1	0.96	0.07	0.15	94.13
BL of UM2	0.94	−0.02	−0.16	90.62
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	0.65	0.47	−0.54	93.60
Hemoglobin, beta (HBB*A)	0.26	0.73	0.63	99.50
MNS system (MS)	−0.90	0.15	0.02	83.52
Rhesus system (cde)	−0.64	0.64	−0.35	93.34
Total contribution (%)	58.37	19.77	14.31	92.45
Cumulative proportion (%)	58.37	78.14	92.45	92.45

[a] The number of populations used is 10. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 14. Solution obtained through the normal varimax rotation of the first three principal components (Table 13) from the ecological correlations on the BL diameters of UM1 and UM2 and allele frequencies for biochemical characters.[a]

Variable	Factor loadings		
	Fac I	II	III
BL of UM1	0.74	0.34	−0.54
BL of UM2	0.65	0.06	−0.69
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	0.03	0.09	−0.96*
Hemoglobin, beta (HBB*A)	0.01	0.99†	−0.08
MNS system (MS)	−0.75	−0.06	0.52
Rhesus system (cde)	−0.96	0.09	−0.10

[a] The cumulative proportion of the three principal components is 92.45%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 15. Principal component analysis of the ecological correlations on shoveling of UI1 and allele frequencies for biochemical characters.[a]

Variable	Factor loadings		Total variance (%)
	PC I	II	
Shoveling	0.96	−0.14	95.04
Properdin factor B, glycine-rich beta-glycoprotein (BF,GBG*S)	0.80	0.01	64.28
Rhesus system (cDE)	0.74	0.65	97.09
Lactase activity (LAA)	−0.90	0.39**	95.79
Total contribution (%)	73.25	14.80	88.05
Cumulative proportion (%)	73.25	88.05	88.05

[a] The number of populations used is 7. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 16. Solution obtained through the normal varimax rotation of the first two principal components (Table 15) from the ecological correlations on shoveling of UI1 and allele frequencies for biochemical characters.[a]

Variable	Factor loadings	
	Fac I	II
Shoveling	0.88	0.41**
Properdin factor B, glycine-rich beta-glycoprotein (BF,GBG*S)	0.66	0.45
Rhesus system (cDE)	0.27	0.95*
Lactase activity (LAA)	−0.96	−0.16

[a] The cumulative proportion of the two principal components is 88.05%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 17. Principal component analysis of the ecological correlations on the Carabelli trait of UM1 and allele frequencies for biochemical characters.[a]

Variable	Factor loadings		Total variance (%)
	PC I	II	
Carabelli trait	0.96	−0.20	95.64
Kidd system (Jk*a)	0.86	0.39	89.74
P system (P*1)	0.34	0.86[†]	86.30
PTC (T)	−0.62	0.72	89.15
Total contribution (%)	53.84	36.37	90.21
Cumulative proportion (%)	53.84	90.21	90.21

[a] The number of populations used is 10. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 18. Solution obtained through the normal varimax rotation of the first two principal components (Table 17) from the ecological correlations on the Carabelli trait of UM1 and allele frequencies for biochemical characters.[a]

Variable	Factor loadings	
	Fac I	II
Carabelli trait	0.91	0.37
Kidd system (Jk*a)	0.50	0.81[†]
P system (P*1)	−0.20	0.91[†]
PTC (T)	−0.91	0.25

[a] The cumulative proportion of the two principal components is 90.21%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

month, average temperature in the coldest month and the amount of annual rainfall, was found to be inversely associated with allele 1 of glyoxalase I and latitude (Tables 25 and 26). Regarding the associations with the ways of life, however, they were not significant at the 5% level (Tables 61 and 62).

Transferrin and the nasal index seemed to constitute a character complex in the second-step analysis (Table 8). But, in the final-step analysis (Tables 27, 28, 63 and 64), such a complex was not confirmed.

Although an inverse association was found between the MD diameter of UI1 and allele B of the ABO system in the second-step analysis (Table 9), further tests of the reality for this character complex were not statistically significant in the final-step analyses (PC II in Table 29 and PC II in Table 65).

The MD diameters of UM1 and UM2 were found to constitute a single character complex together with many biochemical/physiological characters, i.e., allele 1 of haptoglobin-alpha, allele S of properdin factor B glycine-rich beta-glycoprotein, allele Se of the ABH secretion, and allele B of the ABO system (Tables 11 and 12) in the second-step analysis. Also in the final-step analyses, it was confirmed that each of three alleles, i.e., allele 1 of haptoglobin-alpha (the second rotated factor [Fac II] in Table 34), allele S of properdin factor B glycine-rich beta-glycoprotein (PC II in Table 35) and allele B of the ABO system (PC II in Table 39 and Fac II in Table 40), constituted a character complex together with the MD diameters of UM1 and UM2. Among them, however, only one character complex consisting of haptoglobin-alpha allele 1 and the maxillary molar MD diameters was associated with a climatic factor, i.e., average temperature in the coldest month (Fac II in Table 34). None of the above character complexes was associated with any of the ways of life (Tables 69 to 76).

The BL diameters of UM1 and UM2 did not show any significant associations with biochemical/physiological characters in the second-step analyses (Tables 13 and 14). But, in the final-step analysis, one character complex was found. Namely, the BL diameter of UM2 and alleles MS of the MNS system were significantly associated with each other and with the average annual temperature, average temperature in the hottest month, average temperature in the coldest month, and the amount of annual rainfall (PC I in Table 43). On the other hand, there was no character complex consisting of maxillary molar BL diameters and biochemical/physiological characters that is further associated with any of the ways of life (Tables 77 to 82).

UI1 shoveling was found to be significantly associated with alleles cDE of the Rhesus system in the second-step analysis (Fac II in Table 16). But, in the final-step analysis, this character complex was not found to be significantly associated with any natural or cultural environmental variables (Tables 47, 48, 83 and 84).

Lactase activity had a significant inverse corre-

Table 19. Principal component analysis of the ecological correlations on stature, the frequency of CHE2*−, and climatic variables.[a]

Variable	Factor loadings		Total variance (%)
	PC I	II	
Stature	0.46	−0.30	30.20
Cholinesterase 2, pseudocholinesterase 2 (CHE2*−)	0.80**	−0.36	77.41
Latitude	−0.97***	−0.07	95.08
Average annual temperature	0.97***	0.13	95.54
Average temperature in the hottest month	0.93***	−0.08	86.77
Average temperature in the coldest month	0.95***	0.16	93.86
Mean relative annual humidity	−0.33	0.85	82.78
Amount of annual rainfall	0.79	0.55	92.58
Total contribution (%)	65.50	16.28	81.78
Cumulative proportion (%)	65.50	81.78	81.78

[a] The number of populations used is 11. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 20. Solution obtained through the normal varimax rotation of the first two principal components (Table 19) from the ecological correlations on stature, the frequency of CHE2*−, and climatic variables.[a]

Variable	Factor loadings	
	Fac I	II
Stature	0.28	−0.47
Cholinesterase 2, pseudocholinesterase 2 (CHE2*−)	0.56	−0.68
Latitude	−0.91***	0.36
Average annual temperature	0.93***	−0.30
Average temperature in the hottest month	0.80**	−0.48
Average temperature in the coldest month	0.93***	−0.27
Mean relative annual humidity	0.07	0.91
Amount of annual rainfall	0.95***	0.15

[a] The cumulative proportion of the two principal components is 81.78%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 21. Principal component analysis of the ecological correlations on cephalic index, the frequency of PGM1*1, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Cephalic index	−0.62***	−0.13	−0.64	81.79
Phosphoglucomutase 1 (PGM1*1)	0.64*	0.22	0.60	81.77
Latitude	−0.97***	0.13	0.04	95.46
Average annual temperature	0.97***	−0.11	−0.20	98.44
Average temperature in the hottest month	0.87***	−0.42*	−0.14	94.18
Average temperature in the coldest month	0.94***	0.04	−0.22	93.72
Mean relative annual humidity	−0.07	0.98***	−0.11	98.15
Amount of annual rainfall	0.71**	0.57[†]	−0.32	93.56
Total contribution (%)	60.10	19.49	12.54	92.13
Cumulative proportion (%)	60.10	79.59	92.13	92.13

[a] The number of populations used is 18. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 22. Solution obtained through the normal varimax rotation of the first three principal components (Table 21) from the ecological correlations on cephalic index, the frequency of PGM1*1, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
Cephalic index	−0.25**	−0.01	−0.87
Phosphoglucomutase 1 (PGM1*1)	0.26	0.12	0.86
Latitude	−0.89***	0.04	−0.39
Average annual temperature	0.96***	0.01	0.25
Average temperature in the hottest month	0.90***	−0.30*	0.20
Average temperature in the coldest month	0.92***	0.16	0.25
Mean relative annual humidity	−0.19	0.97***	0.05
Amount of annual rainfall	0.67*	0.68*	0.16

[a] The cumulative proportion of the three principal components is 92.13%.
[†] $p<0.10$;* $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 23. Principal component analysis of the ecological correlations on cephalic index, colorblindness, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Cephalic index	−0.55*	0.39	0.57	78.36
Colorblindness (CB)	−0.10	0.72	0.56	84.22
Latitude	−0.95***	0.03	−0.11	92.23
Average annual temperature	0.98***	−0.01	0.11	96.53
Average temperature in the hottest month	0.86***	−0.20	0.40	93.95
Average temperature in the coldest month	0.96***	0.05	−0.01	92.72
Mean relative annual humidity	0.06	0.81*	−0.56	97.60
Amount of annual rainfall	0.78**	0.51[†]	−0.17	90.07
Total contribution (%)	55.73	20.49	14.48	90.71
Cumulative proportion (%)	55.73	76.23	90.71	90.71

[a] The number of populations used is 14. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 24. Solution obtained through the normal varimax rotation of the first three principal components (Table 23) from the ecological correlations on cephalic index, colorblindness, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
Cephalic index	−0.38*	−0.12	0.79
Colorblindness (CB)	0.07	0.20	0.89[†]
Latitude	−0.95***	−0.05	0.14
Average annual temperature	0.97***	0.06	−0.14
Average temperature in the hottest month	0.93***	−0.28	−0.01
Average temperature in the coldest month	0.93***	0.18	−0.18
Mean relative annual humidity	−0.06	0.98*	0.09
Amount of annual rainfall	0.73**	0.61	0.03

[a] The cumulative proportion of the three principal components is 90.71%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 25. Principal component analysis of the ecological correlations on nasal index, the frequency of GLO1*1, and climatic variables.[a]

Variable	Factor loadings		Total variance (%)
	PC I	II	
Nasal index	0.79***	−0.09	62.94
Glyoxalase I (GLO1*1)	−0.69*	0.55*	78.56
Latitude	−0.96***	−0.06	93.25
Average annual temperature	0.98***	0.13	98.32
Average temperature in the hottest month	0.91**	−0.24	88.33
Average temperature in the coldest month	0.94***	0.28***	95.77
Mean relative annual humidity	−0.19	0.95***	93.70
Amount of annual rainfall	0.76*	0.54[†]	86.79
Total contribution (%)	66.36	20.84	87.21
Cumulative proportion (%)	66.36	87.21	87.21

[a] The number of populations used is 11. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 26. Solution obtained through the normal varimax rotation of the first two principal components (Table 25) from the ecological correlations on nasal index, the frequency of GLO1*1, and climatic variables.[a]

Variable	Factor loadings	
	Fac I	II
Nasal index	0.72*	−0.34
Glyoxalase I (GLO1*1)	−0.48*	0.74**
Latitude	−0.93***	0.26
Average annual temperature	0.97***	−0.19
Average temperature in the hottest month	0.78**	−0.52**
Average temperature in the coldest month	0.98***	−0.04
Mean relative annual humidity	0.13	0.96***
Amount of annual rainfall	0.89**	0.27

[a] The cumulative proportion of the two principal components is 87.21%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 27. Principal component analysis of the ecological correlations on nasal index, the frequency of TF*C, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Nasal index	0.71***	−0.10	−0.63	91.83
Transferrin (TF*C)	−0.43	0.58	0.63	91.93
Latitude	−0.97***	0.01	−0.11	94.43
Average annual temperature	0.97***	0.03	0.21	98.40
Average temperature in the hottest month	0.85**	−0.29	0.35	92.65
Average temperature in the coldest month	0.95***	0.16	0.09	93.08
Mean relative annual humidity	−0.08	0.90**	−0.39	96.75
Amount of annual rainfall	0.64[†]	0.73*	0.01	94.03
Total contribution (%)	57.53	22.38	14.23	94.14
Cumulative proportion (%)	57.53	79.91	94.14	94.14

[a] The number of populations used is 15. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 28. Solution obtained through the normal varimax rotation of the first three principal components (Table 27) from the ecological correlations on nasal index, the frequency of TF*C, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
Nasal index	0.40*	0.22	−0.84
Transferrin (TF*C)	−0.11	0.25	0.92
Latitude	−0.93***	−0.04	0.29
Average annual temperature	0.97***	0.03	−0.19
Average temperature in the hottest month	0.90***	−0.32[†]	−0.15
Average temperature in the coldest month	0.92**	0.20	−0.23
Mean relative annual humidity	−0.16	0.97*	0.05
Amount of annual rainfall	0.64[†]	0.73	0.04

[a] The cumulative proportion of the three principal components is 94.14%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 29. Principal component analysis of the ecological correlations on the MD diameter of UI1, the frequency of ABO*B, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UI1	0.34	0.73	0.42	82.57
ABO system (B)	−0.11	−0.81	−0.45	86.15
Latitude	−0.96***	−0.01	0.11	93.50
Average annual temperature	0.99***	0.01	−0.07	98.35
Average temperature in the hottest month	0.85**	−0.02	−0.48	96.22
Average temperature in the coldest month	0.97***	0.05	0.12	96.54
Mean relative annual humidity	0.00	−0.54	0.83[†]	97.51
Amount of annual rainfall	0.68*	−0.57	0.41	95.66
Total contribution (%)	52.04	22.59	18.69	93.31
Cumulative proportion (%)	52.04	74.63	93.31	93.31

[a] The number of populations used is 18. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 30. Solution obtained through the normal varimax rotation of the first three principal components (Table 29) from the ecological correlations on the MD diameter of UI1, the frequency of ABO*B, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UI1	0.20[†]	0.89	−0.01
ABO system (B)	0.03	−0.93	0.07
Latitude	−0.96***	−0.11	−0.05
Average annual temperature	0.98***	0.14	0.08
Average temperature in the hottest month	0.94***	−0.14	−0.25
Average temperature in the coldest month	0.92***	0.26	0.22
Mean relative annual humidity	−0.15	−0.01	0.98[†]
Amount of annual rainfall	0.60*	−0.14	0.76[†]

[a] The cumulative proportion of the three principal components is 93.31%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 31. Principal component analysis of the ecological correlations on the MD diameter of UI1, the frequency of GPT1*1,AAT1*1, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UI1	0.61**	0.49	0.49	85.52
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1, AAT1*1)	0.41	0.57	0.60	86.56
Latitude	−0.95***	0.08	0.05	92.01
Average annual temperature	0.97***	−0.19	−0.07	98.64
Average temperature in the hottest month	0.79**	−0.58†	0.03	96.59
Average temperature in the coldest month	0.97***	0.05	−0.09	95.77
Mean relative annual humidity	−0.12	0.89**	−0.42	98.60
Amount of annual rainfall	0.69*	0.35	−0.60	96.56
Total contribution (%)	55.88	23.42	14.48	93.78
Cumulative proportion (%)	55.88	79.30	93.78	93.78

[a] The number of populations used is 14. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.

† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 32. Solution obtained through the normal varimax rotation of the first three principal components (Table 31) from the ecological correlations on the MD diameter of UI1, the frequency of GPT1*1,AAT1*1, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UI1	0.31*	0.09	0.87†
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	0.08	0.08	0.92†
Latitude	−0.92***	0.03	−0.26
Average annual temperature	0.97***	−0.10	0.20
Average temperature in the hottest month	0.86**	−0.47	−0.02
Average temperature in the coldest month	0.92***	0.09	0.31
Mean relative annual humidity	−0.19	0.96†	0.16
Amount of annual rainfall	0.74†	0.65	0.02

[a] The cumulative proportion of the three principal components is 93.78%.

† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 33. Principal component analysis of the ecological correlations on the MD diameters of UM1 and UM2, the frequency of HPA*1, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UM1	0.44	0.83†	−0.23	93.56
MD of UM2	0.43	0.80†	−0.30	91.95
Haptoglobin, alpha (HPA*1)	0.62	0.58	−0.04	72.99
Latitude	−0.93***	0.24	0.11	93.89
Average annual temperature	0.95***	−0.28	−0.06	98.44
Average temperature in the hottest month	0.73*	−0.60†	−0.25	96.52
Average temperature in the coldest month	0.97***	−0.12	0.03	95.23
Mean relative annual humidity	0.10	0.37	0.91*	97.06
Amount of annual rainfall	0.71**	−0.10	0.67**	95.82
Total contribution (%)	50.37	25.86	16.60	92.83
Cumulative proportion (%)	50.37	76.23	92.83	92.83

[a] The number of populations used is 17. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.

† $p<0.10$;* $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 34. Solution obtained through the normal varimax rotation of the first three principal components (Table 33) from the ecological correlations on the MD diameters of UM1 and UM2, the frequency of HPA*1, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UM1	0.04	0.97*	0.04
MD of UM2	0.04	0.96†	−0.03
Haptoglobin, alpha (HPA*1)	0.29	0.77*	0.21
Latitude	−0.95**	−0.21	−0.04
Average annual temperature	0.97**	0.17	0.09
Average temperature in the hottest month	0.95***	−0.15	−0.22*
Average temperature in the coldest month	0.91**	0.29*	0.21
Mean relative annual humidity	−0.16	0.11	0.97*
Amount of annual rainfall	0.61*	0.02	0.76†

[a] The cumulative proportion of the three principal components is 92.83%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 35. Principal component analysis of the ecological correlations on the MD diameters of UM1 and UM2, the frequency of BF,GBG*S, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UM1	0.11	0.88**	−0.40	94.02
MD of UM2	0.10	0.86**	−0.40	90.93
Properdin factor B, glycine-rich beta-glycoprotein (BF,GBG*S)	−0.24	0.72**	−0.05	58.28
Latitude	−0.96***	0.06	0.12	94.40
Average annual temperature	0.99***	−0.01	−0.07	99.35
Average temperature in the hottest month	0.87†	−0.40	−0.13	93.63
Average temperature in the coldest month	0.96***	0.14	0.01	94.65
Mean relative annual humidity	−0.02	0.69	0.70	96.25
Amount of annual rainfall	0.76†	0.38	0.49	97.43
Total contribution (%)	47.41	31.48	12.09	90.99
Cumulative proportion (%)	47.41	78.90	90.99	90.99

[a] The number of populations used is 13. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 36. Solution obtained through the normal varimax rotation of the first three principal components (Table 35) from the ecological correlations on the MD diameters of UM1 and UM2, the frequency of BF,GBG*S, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UM1	0.10	0.96*	0.09
MD of UM2	0.09	0.95*	0.08
Properdin factor B, glycine-rich beta-glycoprotein (BF,GBG*S)	−0.27	0.65	0.29
Latitude	−0.97**	−0.01	0.04
Average annual temperature	1.00**	0.03	0.02
Average temperature in the hottest month	0.90**	−0.28*	−0.23
Average temperature in the coldest month	0.95**	0.12	0.16
Mean relative annual humidity	−0.11	0.26	0.94†
Amount of annual rainfall	0.70†	0.09	0.69†

[a] The cumulative proportion of the three principal components is 90.99%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 37. Principal component analysis of the ecological correlations on the MD diameters of UM1 and UM2, the frequency of Se, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UM1	0.53	0.78	0.27	96.10
MD of UM2	0.57	0.77	0.11	92.69
ABH secretion (Se)	−0.00	0.94	0.03	88.83
Latitude	−0.96***	0.15	0.08	94.89
Average annual temperature	0.99***	−0.09	−0.06	99.37
Average temperature in the hottest month	0.82**	−0.28	−0.46*	96.68
Average temperature in the coldest month	0.97***	−0.05	0.09	96.03
Mean relative annual humidity	−0.09	−0.25	0.95**	97.61
Amount of annual rainfall	0.70*	−0.51	0.44*	94.51
Total contribution (%)	51.58	27.98	15.63	95.19
Cumulative proportion (%)	51.58	79.56	95.19	95.19

[a] The number of populations used is 13. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.

[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 38. Solution obtained through the normal varimax rotation of the first three principal components (Table 37) from the ecological correlations on the MD diameters of UM1 and UM2, the frequency of Se, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UM1	0.26	0.94[†]	0.09
MD of UM2	0.31	0.91[†]	−0.06
ABH secretion (Se)	−0.28	0.88	−0.18
Latitude	−0.96**	−0.14	0.03
Average annual temperature	0.98**	0.20	−0.02
Average temperature in the hottest month	0.91[†]	−0.11	−0.37*
Average temperature in the coldest month	0.94**	0.27*	0.11
Mean relative annual humidity	−0.09	−0.06	0.98[†]
Amount of annual rainfall	0.78	−0.17	0.55[†]

[a] The cumulative proportion of the three principal components is 95.19%.

[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 39. Principal component analysis of the ecological correlations on the MD diameters of UM1 and UM2, the frequency of ABO*B, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UM1	0.38	0.90*	0.02	95.34
MD of UM2	0.37	0.88*	−0.05	91.63
ABO system (B)	−0.18	−0.90**	0.18	87.53
Latitude	−0.95***	0.16	0.12	93.72
Average annual temperature	0.97***	−0.16	−0.09	98.46
Average temperature in the hottest month	0.79[†]	−0.45	−0.37*	96.23
Average temperature in the coldest month	0.98***	−0.03	0.03	95.45
Mean relative annual humidity	0.06	0.14	0.98***	97.85
Amount of annual rainfall	0.70*	−0.22	0.64**	95.76
Total contribution (%)	47.14	30.12	17.41	94.66
Cumulative proportion (%)	47.14	77.26	94.66	94.66

[a] The number of populations used is 17. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.

[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 40. Solution obtained through the normal varimax rotation of the first three principal components (Table 39) from the ecological correlations on the MD diameters of UM1 and UM2, the frequency of ABO*B, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UM1	0.11	0.96***	0.12
MD of UM2	0.12	0.95***	0.05
ABO system (B)	0.05	−0.93***	0.11
Latitude	−0.96***	−0.11	−0.04
Average annual temperature	0.98***	0.11	0.07
Average temperature in the hottest month	0.93***	−0.19	−0.24***
Average temperature in the coldest month	0.93**	0.23	0.20
Mean relative annual humidity	−0.14	0.06	0.98***
Amount of annual rainfall	0.63*	−0.08	0.75**

[a] The cumulative proportion of the three principal components is 94.66%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 41. Principal component analysis of the ecological correlations on the BL diameters of UM1 and UM2, the frequency of GPT1*1,AAT1*1, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
BL of UM1	0.56	0.70[†]	−0.28	87.74
BL of UM2	0.54	0.70[†]	−0.31	88.47
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	0.49	0.59[†]	−0.39	74.13
Latitude	−0.93***	0.22	−0.03	92.52
Average annual temperature	0.93***	−0.35	0.05	98.22
Average temperature in the hottest month	0.72[†]	−0.64	−0.18	96.29
Average temperature in the coldest month	0.95***	−0.14	0.14	94.49
Mean relative annual humidity	−0.04	0.73	0.67	97.47
Amount of annual rainfall	0.73[†]	0.13	0.64	95.14
Total contribution (%)	50.36	27.53	13.71	91.61
Cumulative proportion (%)	50.36	77.90	91.61	91.61

[a] The number of populations used is 14. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 42. Solution obtained through the normal varimax rotation of the first three principal components (Table 41) from the ecological correlations on the BL diameters of UM1 and UM2, the frequency of GPT1*1,AAT1*1, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
BL of UM1	0.15	0.91[†]	0.17
BL of UM2	0.13	0.92[†]	0.14
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	0.12	0.85[†]	0.01
Latitude	−0.93***	−0.24	0.02
Average annual temperature	0.98***	0.13	−0.07
Average temperature in the hottest month	0.88***	−0.06	−0.43
Average temperature in the coldest month	0.93***	0.26[†]	0.12
Mean relative annual humidity	−0.22	0.19	0.94[†]
Amount of annual rainfall	0.70*	0.11	0.67

[a] The cumulative proportion of the three principal components is 91.61%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 43. Principal component analysis of the ecological correlations on the BL diameters of UM1 and UM2, the frequency of MS, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
BL of UM1	0.50[†]	0.64	−0.52	93.65
BL of UM2	0.54*	0.54	−0.61	95.06
MNS system (MS)	−0.66**	−0.48	−0.10	67.22
Latitude	−0.92***	0.28	0.02	93.12
Average annual temperature	0.93***	−0.31*	0.05	97.21
Average temperature in the hottest month	0.79**	−0.55[†]	−0.12	93.45
Average temperature in the coldest month	0.94***	−0.15	0.09	90.92
Mean relative annual humidity	0.08	0.64	0.72	94.53
Amount of annual rainfall	0.76*	0.18	0.59	96.09
Total contribution (%)	53.27	20.80	17.18	91.25
Cumulative proportion (%)	53.27	74.07	91.25	91.25

[a] The number of populations used is 16. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 44. Solution obtained through the normal varimax rotation of the first three principal components (Table 43) from the ecological correlations on the BL diameters of UM1 and UM2, the frequency of MS, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
BL of UM1	0.10	0.96*	0.09
BL of UM2	0.17	0.96[†]	−0.03
MNS system (MS)	−0.35	−0.53	−0.52
Latitude	−0.94***	−0.21[†]	−0.07
Average annual temperature	0.97***	0.15	0.11
Average temperature in the hottest month	0.95***	0.04	−0.20
Average temperature in the coldest month	0.90***	0.23*	0.23
Mean relative annual humidity	−0.20	0.01	0.95[†]
Amount of annual rainfall	0.61*	0.07	0.76*

[a] The cumulative proportion of the three principal components is 91.25%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 45. Principal component analysis of the ecological correlations on the BL diameters of UM1 and UM2, the frequency of cde, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
BL of UM1	0.50[†]	0.64	0.53	94.25
BL of UM2	0.52[†]	0.52	0.62	93.13
Rhesus system (cde)	−0.46	−0.59	0.10	56.50
Latitude	−0.93***	0.26	−0.01	93.17
Average annual temperature	0.95***	−0.28	−0.06	98.11
Average temperature in the hottest month	0.80**	−0.52	0.11	91.96
Average temperature in the coldest month	0.94***	−0.14	−0.10	91.98
Mean relative annual humidity	0.06	0.64	−0.71	91.23
Amount of annual rainfall	0.76**	0.21	−0.59	96.07
Total contribution (%)	50.98	21.43	17.19	89.60
Cumulative proportion (%)	50.98	72.41	89.60	89.60

[a] The number of populations used is 16. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 46. Solution obtained through the normal varimax rotation of the first three principal components (Table 45) from the ecological correlations on the BL diameters of UM1 and UM2, the frequency of cde, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
BL of UM1	0.11	0.96*	−0.11
BL of UM2	0.18	0.95†	0.03
Rhesus system (cde)	−0.15	−0.50	0.54
Latitude	−0.94***	−0.20	0.05
Average annual temperature	0.97***	0.14	−0.10
Average temperature in the hottest month	0.93***	0.03	0.21
Average temperature in the coldest month	0.91***	0.21	−0.21
Mean relative annual humidity	−0.18	−0.01	−0.94†
Amount of annual rainfall	0.63*	0.06	−0.75*

[a] The cumulative proportion of the three principal components is 89.60%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 47. Principal component analysis of the ecological correlations on shoveling of UI1, the frequency of cDE, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Shoveling	−0.07	0.92*	0.27	92.40
Rhesus system (cDE)	−0.56	0.72	0.13	85.56
Latitude	−0.96***	−0.10	0.07	93.45
Average annual temperature	0.98***	0.13	−0.06	97.49
Average temperature in the hottest month	0.88**	0.23	−0.33	92.71
Average temperature in the coldest month	0.96***	0.01	0.04	91.63
Mean relative annual humidity	−0.01	−0.32	0.94*	98.17
Amount of annual rainfall	0.73**	0.07	0.65*	95.84
Total contribution (%)	55.19	19.38	18.84	93.41
Cumulative proportion (%)	55.19	74.57	93.41	93.41

[a] The number of populations used is 15. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 48. Solution obtained through the normal varimax rotation of the first three principal components (Table 47) from the ecological correlations on shoveling of UI1, the frequency of cDE, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
Shoveling	0.10	0.95†	0.05
Rhesus system (cDE)	−0.40	0.82	−0.11
Latitude	−0.96***	0.10	−0.04
Average annual temperature	0.98***	−0.08	0.05
Average temperature in the hottest month	0.93***	−0.03	−0.25
Average temperature in the coldest month	0.93***	−0.16	0.16
Mean relative annual humidity	−0.15	−0.07	0.98†
Amount of annual rainfall	0.67	0.09	0.71†

[a] The cumulative proportion of the three principal components is 93.41%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 49. Principal component analysis of the ecological correlations on shoveling of UI1, the frequency of LAA, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Shoveling	−0.36	−0.90	−0.05	95.15
Lactase activity (LAA)	−0.09	0.97[†]	−0.09	95.66
Latitude	−0.95***	0.21	0.07	94.66
Average annual temperature	0.99***	0.04	−0.05	98.82
Average temperature in the hottest month	0.88***	−0.11	−0.42***	95.54
Average temperature in the coldest month	0.96***	0.17	0.11	96.62
Mean relative annual humidity	−0.10	0.07	0.99***	98.65
Amount of annual rainfall	0.76*	−0.18	0.59**	95.87
Total contribution (%)	53.86	23.51	19.00	96.37
Cumulative proportion (%)	53.86	77.37	96.37	96.37

[a] The number of populations used is 10. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 50. Solution obtained through the normal varimax rotation of the first three principal components (Table 49) from the ecological correlations on shoveling of UI1, the frequency of LAA, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
Shoveling	−0.28	−0.93	−0.08
Lactase activity (LAA)	−0.17	0.96	−0.07
Latitude	−0.96***	0.12	0.05
Average annual temperature	0.99***	0.13	−0.03
Average temperature in the hottest month	0.89***	−0.02	−0.39*
Average temperature in the coldest month	0.94***	0.25	0.14
Mean relative annual humidity	−0.13	0.03	0.98**
Amount of annual rainfall	0.76*	−0.12	0.60*

[a] The cumulative proportion of the three principal components is 96.37%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 51. Principal component analysis of the ecological correlations on the Carabelli trait of UM1, the frequency of Jk*a, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Carabelli trait	−0.53	0.59	−0.51	89.35
Kidd system (Jk*a)	−0.24	0.78*	−0.48	89.60
Latitude	−0.94***	−0.10	0.06	89.02
Average annual temperature	0.96***	0.14	−0.19	98.14
Average temperature in the hottest month	0.88**	−0.31	−0.32	97.44
Average temperature in the coldest month	0.91***	0.36*	−0.09	96.12
Mean relative annual humidity	−0.16	0.74*	0.65	98.76
Amount of annual rainfall	0.80***	0.42	0.39	96.97
Total contribution (%)	55.14	24.13	15.16	94.43
Cumulative proportion (%)	55.14	79.26	94.43	94.43

[a] The number of populations used is 12. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 52. Solution obtained through the normal varimax rotation of the first three principal components (Table 51) from the ecological correlations on the Carabelli trait of UM1, the frequency of Jk*a, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
Carabelli trait	−0.28	0.90[†]	0.04
Kidd system (Jk*a)	0.05	0.93*	0.15
Latitude	−0.93***	0.17	0.06
Average annual temperature	0.98***	−0.06	−0.14
Average temperature in the hottest month	0.79**	−0.27	−0.52[†]
Average temperature in the coldest month	0.98***	0.04	0.08
Mean relative annual humidity	−0.03	0.16	0.98*
Amount of annual rainfall	0.83**	−0.18	0.50

[a] The cumulative proportion of the three principal components is 94.43%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 53. Principal component analysis of the ecological correlations on the Carabelli trait of UM1, the frequency of T, and climatic variables.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Carabelli trait	−0.25	0.55	0.75	92.64
PTC (T)	0.63[†]	−0.57	−0.38	86.36
Latitude	−0.95***	0.01	−0.12	92.02
Average annual temperature	0.96***	0.14	0.23	98.71
Average temperature in the hottest month	0.89***	−0.23	0.28	92.48
Average temperature in the coldest month	0.91***	0.29	0.18	95.13
Mean relative annual humidity	−0.00	0.76	−0.63	96.83
Amount of annual rainfall	0.79**	0.41	−0.41	95.14
Total contribution (%)	56.63	19.00	18.03	93.66
Cumulative proportion (%)	56.63	75.63	93.66	93.66

[a] The number of populations used is 15. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 54. Solution obtained through the normal varimax rotation of the first three principal components (Table 53) from the ecological correlations on the Carabelli trait of UM1, the frequency of T, and climatic variables.[a]

Variable	Factor loadings		
	Fac I	II	III
Carabelli trait	0.06	0.96	0.10
PTC (T)	0.41	−0.83	0.12
Latitude	−0.93***	0.22	−0.00
Average annual temperature	0.99***	−0.05	−0.04
Average temperature in the hottest month	0.89***	−0.24	0.27
Average temperature in the coldest month	0.96***	0.03	−0.18
Mean relative annual humidity	−0.08	0.05	−0.98*
Amount of annual rainfall	0.68*	−0.26	−0.65

[a] The cumulative proportion of the three principal components is 93.66%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

lation with shoveling in the first-step analysis (Table 2). This character complex seems to be present also in both second-step (PC I in Table 15 and Fac I in Table 16) and final-step (PC II in Table 49, Fac II in Table 50, PC I in Table 85, and Fac I in Table 86) analyses, but their statistical significance was not proven. Therefore, it is unclear whether or not there are any associations with natural and/or cultural environmental factors.

A few character complexes containing the Carabelli trait of UM1 were suggested in the second-step analyses (Tables 17 and 18), but their existence was not shown to be statistically significant. In the final-step analyses, however, it was found that the Carabelli trait and allele Jk*a of the Kidd system constituted a character complex (Tables 87 and 88) and the complex might be associated with hunting-gathering (Table 87) or milking (Table 88).

Discussion

The present research is fairly preliminary and based on only broadly collected data from the literature. Nevertheless, it showed that some morphological characters were significantly associated with biochemical/physiological characters and, further, both were associated with natural and/or cultural environmental factors.

In general, an ecological or among-group correlation between a character and an environmental factor is considered to have resulted from one or more of three basic evolutionary causes, i.e., adaptation to local environments through natural selection, random genetic drift, and gene flow (i.e., migration and/or hybridization with other populations), as suggested by many authors (e.g., Stern, 1960; Dobzhansky, 1963; Mettler and Gregg, 1969; Harrison *et al.*, 1977; Molnar, 1992; Marks, 1995). Although it is very difficult in practice to determine causes for such an ecological correlation, some ecological correlations can be explained. For example, let us assume that genetic drift occurred that regarded a major gene of a certain monogenic or oligogenic character like a blood-group system when a small-sized population migrated to another region. In this case, an allele for the monogenic or oligogenic character changes to another allele and, as a result, the phenotype drastically changes. But a morphological character controlled by polygenes with a minor and averaged effect may cause limited changes to the phenotype because most of the migrants share substantially similar combinations of alleles across the relevant polygenic sites with most members of the population from which they originally came even if half of the polygenic sites were affected by genetic drift. In a case like this, it is expected that the ecological correlation between the monogenic or oligogenic character and an environmental factor such as average annual temperature may be significant, but the ecological correlation between the morphological character and the environmental factor or between the morphological and the monogenic or oligogenic characters is close to zero.

On the other hand, if geographical variations of two or more characters, whether controlled by a major gene or polygenes, are resultant phenomena of adaptation to an environmental factor, the ecological correlations of these characters with one another and with the environmental factor may both be significant.

Further, as was suggested by Sakura (2002), if a recent gene flow is a main cause for geographical clines in gene frequency or phenotypic value, the directions of the clines for most characters should be consistent with one another. Also in this case, the ecological correlations of the characters with one another and with some environmental factors may both be significant.

There are also some other possible causes for an ecological correlation between two characters: pleiotropic genes, linkage of genes, the state of two characters being elements in the same ontogenetic process or physiological cycle, etc. However, detailed examination for these possible causes is a task to be carried out in the future.

In the following sections, remarkable findings in the present preliminary analyses are discussed briefly.

Table 55. Principal component analysis of the ecological correlations on stature, the frequency of CHE2*−, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Stature	0.09	0.65	0.71*	93.00
Cholinesterase 2, pseudocholinesterase 2 (CHE2*−)	0.12	0.93	−0.22	92.01
Hunting-gathering	−0.93	0.08	0.24	92.26
Cattle breeding	0.88	0.05	−0.11	78.93
Milking	0.52	−0.37	0.72[†]	91.78
Agriculture	0.88	0.05	−0.11	78.93
Total contribution (%)	44.95	23.84	19.03	87.82
Cumulative proportion (%)	44.95	68.79	87.82	87.82

[a] The number of populations used is 11. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 56. Solution obtained through the normal varimax rotation of the first three principal components (Table 55) from the ecological correlations on stature, the frequency of CHE2*−, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
Stature	−0.03	−0.01	0.96*
Cholinesterase 2, pseudocholinesterase 2 (CHE2*−)	0.20	0.80	0.49
Hunting-gathering	−0.95	0.07	0.11
Cattle breeding	0.88	−0.04	0.08
Milking	0.33	−0.83	0.33
Agriculture	0.88	−0.04	0.08

[a] The cumulative proportion of the three principal components is 87.82%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 57. Principal component analysis of the ecological correlations on cephalic index, the frequency of PGM1*1, and the ways of life.[a]

Variable	Factor loadings				Total variance (%)
	PC I	II	III	IV	
Cephalic index	−0.03	0.74	0.65	0.08	97.68
Phosphoglucomutase 1 (PGM1*1)	0.61	−0.34	0.40	0.55	94.75
Hunting-gathering	0.83	−0.38	0.16	−0.27	92.99
Cattle breeding	−0.81	−0.00	0.15	−0.08	69.27
Milking	−0.47	−0.55	0.53	−0.39	95.11
Agriculture	−0.73	−0.39	−0.02	0.48	91.53
Total contribution (%)	41.24	20.86	15.36	12.75	90.22
Cumulative proportion (%)	41.24	62.10	77.47	90.22	90.22

[a] The number of populations used is 18. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 58. Solution obtained through the normal varimax rotation of the first four principal components (Table 57) from the ecological correlations on cephalic index, the frequency of PGM1*1, and the ways of life.[a]

Variable	Factor loadings			
	Fac I	II	III	IV
Cephalic index	0.02	0.02	0.99*	0.00
Phosphoglucomutase 1 (PGM1*1)	0.12	0.06	0.03	0.96*
Hunting-gathering	0.79	−0.12	−0.24	0.49
Cattle breeding	−0.57	−0.43	0.14	−0.40
Milking	−0.13	−0.97*	−0.05	−0.03
Agriculture	−0.89	−0.25	−0.22	0.07

[a] The cumulative proportion of the four principal components is 90.22%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 59. Principal component analysis of the ecological correlations on cephalic index, colorblindness, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Cephalic index	−0.29	0.62	0.72	98.95
Colorblindness (CB)	−0.81	−0.21	−0.18	72.56
Hunting-gathering	0.89	0.20	−0.31	92.94
Cattle breeding	−0.83	0.19	−0.29	80.74
Milking	−0.33	0.79	−0.44	93.55
Agriculture	−0.76	−0.33	0.05	69.49
Total contribution (%)	48.54	20.65	15.52	84.70
Cumulative proportion (%)	48.54	69.18	84.70	84.70

[a] The number of populations used is 14. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 60. Solution obtained through the normal varimax rotation of the first three principal components (Table 59) from the ecological correlations on cephalic index, colorblindness, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
Cephalic index	−0.06	0.14	0.98*
Colorblindness (CB)	−0.82	0.20	−0.10
Hunting-gathering	0.91	0.05	−0.32
Cattle breeding	−0.70	0.57	0.03
Milking	−0.00	0.96*	0.14
Agriculture	−0.83	−0.04	0.01

[a] The cumulative proportion of the three principal components is 84.70%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 61. Principal component analysis of the ecological correlations on nasal index, the frequency of GLO1*1, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Nasal index	0.03	−0.39	0.84	85.94
Glyoxalase I (GLO1*1)	−0.22	0.86*	−0.07	79.60
Hunting-gathering	−0.81	0.24	0.40	87.38
Cattle breeding	0.81	0.37	−0.13	80.28
Milking	0.15	0.82	0.43	87.73
Agriculture	0.87	−0.03	0.37	88.97
Total contribution (%)	35.60	29.24	20.14	84.98
Cumulative proportion (%)	35.60	64.84	84.98	84.98

[a] The number of populations used is 11. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 62. Solution obtained through the normal varimax rotation of the first three principal components (Table 61) from the ecological correlations on nasal index, the frequency of GLO1*1, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
Nasal index	−0.07	−0.07	0.92
Glyoxalase I (GLO1*1)	−0.15	0.79	−0.39
Hunting-gathering	−0.83	0.39	0.20
Cattle breeding	0.84	0.27	−0.16
Milking	0.17	0.91*	0.14
Agriculture	0.83	0.07	0.45

[a] The cumulative proportion of the three principal components is 84.98%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 63. Principal component analysis of the ecological correlations on nasal index, the frequency of TF*C, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Nasal index	−0.66	−0.47	0.33	77.10
Transferrin (TF*C)	0.39	0.82	−0.02	82.30
Hunting-gathering	−0.81	0.25	0.43	90.83
Cattle breeding	0.88	−0.19	−0.02	81.32
Milking	0.67	0.23	0.68[†]	96.70
Agriculture	0.77	−0.54	0.18	92.28
Total contribution (%)	51.26	22.23	13.26	86.76
Cumulative proportion (%)	51.26	73.50	86.76	86.76

[a] The number of populations used is 15. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 64. Solution obtained through the normal varimax rotation of the first three principal components (Table 63) from the ecological correlations on nasal index, the frequency of TF*C, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
Nasal index	−0.40	−0.78	−0.04
Transferrin (TF*C)	−0.09	0.87	0.24
Hunting-gathering	−0.92	−0.25	0.08
Cattle breeding	0.81	0.21	0.33
Milking	0.21	0.26	0.92[†]
Agriculture	0.84	−0.20	0.42

[a] The cumulative proportion of the three principal components is 86.76%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 65. Principal component analysis of the ecological correlations on the MD diameter of UI1, the frequency of ABO*B, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UI1	−0.25	−0.90	−0.03	86.47
ABO system (B)	0.53	0.63	0.40	84.18
Hunting-gathering	−0.83	−0.04	0.45*	89.08
Cattle breeding	0.78	−0.42	−0.10	80.22
Milking	0.50	−0.44	0.71**	93.96
Agriculture	0.89	−0.05	−0.14	80.46
Total contribution (%)	44.55	26.20	14.98	85.73
Cumulative proportion (%)	44.55	70.75	85.73	85.73

[a] The number of populations used is 18. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 66. Solution obtained through the normal varimax rotation of the first three principal components (Table 65) from the ecological correlations on the MD diameter of UI1, the frequency of ABO*B, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UI1	−0.05	−0.89	0.27
ABO system (B)	0.16	0.87	0.26
Hunting-gathering	−0.92	−0.18	0.10
Cattle breeding	0.80	−0.13	0.37
Milking	0.18	−0.00	0.95[†]
Agriculture	0.84	0.22	0.22

[a] The cumulative proportion of the three principal components is 85.73%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 67. Principal component analysis of the ecological correlations on the MD diameter of UI1, the frequency of GPT1*1,AAT1*1, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UI1	0.15	0.90**	−0.24	88.38
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1, AAT1*1)	−0.62	0.49	−0.39	77.27
Hunting-gathering	−0.79	0.25	0.46	88.98
Cattle breeding	0.88	0.19	−0.17	83.75
Milking	0.51	0.51	0.64	93.01
Agriculture	0.86	−0.08	−0.02	74.43
Total contribution (%)	46.57	23.40	14.33	84.30
Cumulative proportion (%)	46.57	69.97	84.30	84.30

[a] The number of populations used is 14. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 68. Solution obtained through the normal varimax rotation of the first three principal components (Table 67) from the ecological correlations on the MD diameter of UI1, the frequency of GPT1*1,AAT1*1, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UI1	0.13	0.88	0.29
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1,AAT1*1)	−0.45	0.68	−0.34
Hunting-gathering	−0.93	0.09	0.14
Cattle breeding	0.84	0.15	0.33
Milking	0.14	0.10	0.95[†]
Agriculture	0.79	−0.15	0.31

[a] The cumulative proportion of the three principal components is 84.30%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 69. Principal component analysis of the ecological correlations on the MD diameters of UM1 and UM2, the frequency of HPA*1, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UM1	−0.75	0.36	−0.39	84.60
MD of UM2	−0.60	0.75[†]	0.04	93.45
Haptoglobin, alpha (HPA*1)	−0.42	0.85*	0.01	90.48
Hunting-gathering	−0.83	−0.18	0.42	89.89
Cattle breeding	0.78	0.47	−0.08	83.59
Milking	0.42	0.45	0.74	93.15
Agriculture	0.71	0.52	−0.23	82.88
Total contribution (%)	43.94	30.93	13.43	88.29
Cumulative proportion (%)	43.94	74.86	88.29	88.29

[a] The number of populations used is 17. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 70. Solution obtained through the normal varimax rotation of the first three principal components (Table 69) from the ecological correlations on the MD diameters of UM1 and UM2, the frequency of HPA*1, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UM1	−0.24	0.75	−0.48
MD of UM2	−0.13	0.95[†]	0.08
Haptoglobin, alpha (HPA*1)	0.07	0.94[†]	0.14
Hunting-gathering	−0.91	0.27	0.05
Cattle breeding	0.85	−0.03	0.33
Milking	0.20	0.08	0.94[†]
Agriculture	0.89	0.06	0.19

[a] The cumulative proportion of the three principal components is 88.29%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 71. Principal component analysis of the ecological correlations on the MD diameters of UM1 and UM2, the frequency of BF,GBG*S, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UM1	−0.75	0.25	0.52	89.47
MD of UM2	−0.47	0.85*	0.06	95.37
Properdin factor B, glycine-rich beta-glycoprotein (BF,GBG*S)	−0.79	0.04	0.11	63.71
Hunting-gathering	−0.87	0.00	−0.39	90.54
Cattle breeding	0.77	0.18	0.19	66.56
Milking	0.51	0.54	−0.62	93.83
Agriculture	0.78	0.27	0.43	87.11
Total contribution (%)	51.79	17.13	14.88	83.80
Cumulative proportion (%)	51.79	68.92	83.80	83.80

[a] The number of populations used is 13. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 72. Solution obtained through the normal varimax rotation of the first three principal components (Table 71) from the ecological correlations on the MD diameters of UM1 and UM2, the frequency of BF,GBG*S, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UM1	−0.24	0.67	0.62
MD of UM2	−0.13	0.96*	−0.13
Properdin factor B, glycine-rich beta-glycoprotein (BF,GBG*S)	−0.55	0.41	0.41
Hunting-gathering	−0.90	0.29	0.07
Cattle breeding	0.76	−0.14	−0.26
Milking	0.18	0.10	−0.95
Agriculture	0.93	0.00	−0.12

[a] The cumulative proportion of the three principal components is 83.80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 73. Principal component analysis of the ecological correlations on the MD diameters of UM1 and UM2, the frequency of Se, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UM1	−0.54	0.64	−0.26	77.19
MD of UM2	−0.38	0.88*	−0.01	91.60
ABH secretion (Se)	−0.68	0.14	−0.54	77.67
Hunting-gathering	−0.78	0.03	0.57	92.64
Cattle breeding	0.79	0.33	−0.24	78.35
Milking	0.34	0.55	0.69	89.29
Agriculture	0.80	0.44	−0.15	85.72
Total contribution (%)	41.28	25.72	17.63	84.64
Cumulative proportion (%)	41.28	67.01	84.64	84.64

[a] The number of populations used is 13. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 74. Solution obtained through the normal varimax rotation of the first three principal components (Table 73) from the ecological correlations on the MD diameters of UM1 and UM2, the frequency of Se, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UM1	−0.11	0.86	−0.12
MD of UM2	−0.03	0.93[†]	0.24
ABH secretion (Se)	−0.24	0.57	−0.63
Hunting-gathering	−0.90	0.26	0.22
Cattle breeding	0.86	−0.04	0.21
Milking	0.11	0.13	0.93
Agriculture	0.86	0.02	0.35

[a] The cumulative proportion of the three principal components is 84.64%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 75. Principal component analysis of the ecological correlations on the MD diameters of UM1 and UM2, the frequency of ABO*B, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
MD of UM1	−0.70	0.43	−0.34	79.57
MD of UM2	−0.52	0.77	0.08	86.91
ABO system (B)	0.57	−0.49	0.05	56.95
Hunting-gathering	−0.84	−0.12	0.43	89.72
Cattle breeding	0.79	0.45	−0.09	83.05
Milking	0.47	0.39	0.76[†]	95.45
Agriculture	0.77	0.44	−0.20	83.70
Total contribution (%)	46.11	22.64	13.44	82.19
Cumulative proportion (%)	46.11	68.75	82.19	82.19

[a] The number of populations used is 17. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 76. Solution obtained through the normal varimax rotation of the first three principal components (Table 75) from the ecological correlations on the MD diameters of UM1 and UM2, the frequency of ABO*B, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
MD of UM1	−0.17	0.79	−0.37
MD of UM2	−0.05	0.91	0.18
ABO system (B)	0.18	−0.73	0.05
Hunting-gathering	−0.88	0.34	0.09
Cattle breeding	0.85	−0.08	0.31
Milking	0.21	−0.05	0.95*
Agriculture	0.89	−0.07	0.20

[a] The cumulative proportion of the three principal components is 82.19%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 77. Principal component analysis of the ecological correlations on the BL diameters of UM1 and UM2, the frequency of GPT1*1,AAT1*1, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
BL of UM1	−0.68	0.51	0.19	76.27
BL of UM2	−0.51	0.62	−0.02	64.40
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1, AAT1*1)	−0.78	0.29	0.40	86.02
Hunting-gathering	−0.70	−0.47	0.31	81.22
Cattle breeding	0.72	0.57	0.14	85.15
Milking	0.57	−0.26	0.76	97.31
Agriculture	0.77	0.39	0.15	77.19
Total contribution (%)	46.58	21.33	13.16	81.08
Cumulative proportion (%)	46.58	67.92	81.08	81.08

[a] The number of populations used is 14. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 78. Solution obtained through the normal varimax rotation of the first three principal components (Table 77) from the ecological correlations on the BL diameters of UM1 and UM2, the frequency of GPT1*1,AAT1*1, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
BL of UM1	−0.14	0.85	−0.15
BL of UM2	0.07	0.73	−0.32
Glutamic-pyruvate transaminase, alanine aminotransferase (GPT1*1, AAT1*1)	−0.39	0.84	0.06
Hunting-gathering	−0.85	0.24	0.18
Cattle breeding	0.90	−0.01	0.22
Milking	0.19	−0.24	0.94[†]
Agriculture	0.82	−0.16	0.29

[a] The cumulative proportion of the three principal components is 81.08%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 79. Principal component analysis of the ecological correlations on the BL diameters of UM1 and UM2, the frequency of MS, and the ways of life.[a]

Variable	Factor loadings				Total variance (%)
	PC I	II	III	IV	
BL of UM1	−0.60	0.50	0.00	0.09	62.02
BL of UM2	−0.52	0.44	0.60	−0.34	93.48
MNS system (MS)	0.52	−0.44	0.60	0.34	93.48
Hunting-gathering	−0.73	−0.47	−0.00	−0.43*	94.44
Cattle breeding	0.76	0.46	0.31	−0.18	91.20
Milking	0.67	−0.43	−0.00	−0.51†	89.75
Agriculture	0.76	0.46	−0.31	−0.18	91.20
Total contribution (%)	43.30	21.02	12.82	10.80	87.94
Cumulative proportion (%)	43.30	64.31	77.14	87.94	87.94

[a] The number of populations used is 16. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 80. Solution obtained through the normal varimax rotation of the first four principal components (Table 79) from the ecological correlations on the BL diameters of UM1 and UM2, the frequency of MS, and the ways of life.[a]

Variable	Factor loadings			
	Fac I	II	III	IV
BL of UM1	−0.09	0.33	−0.33	0.62
BL of UM2	−0.10	0.93†	−0.08	0.25
MNS system (MS)	0.10	−0.08	0.93	−0.25
Hunting-gathering	−0.88	0.28	–0.28	−0.16
Cattle breeding	0.86	0.24	0.19	−0.28
Milking	0.17	−0.12	0.12	−0.92*
Agriculture	0.86	−0.19	−0.24	−0.28

[a] The cumulative proportion of the four principal components is 87.94%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 81. Principal component analysis of the ecological correlations on the BL diameters of UM1 and UM2, the frequency of cde, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
BL of UM1	−0.61	−0.46	0.17	61.38
BL of UM2	−0.46	−0.26	0.80*	90.81
Rhesus system (cde)	0.72**	0.41	0.45	89.34
Hunting-gathering	−0.66†	0.61	0.19	84.58
Cattle breeding	0.77**	−0.43	0.36	90.31
Milking	0.75**	0.51	0.13	83.95
Agriculture	0.74*	−0.47	−0.14	78.98
Total contribution (%)	46.40	21.20	15.17	82.76
Cumulative proportion (%)	46.40	67.60	82.76	82.76

[a] The number of populations used is 16. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 82. Solution obtained through the normal varimax rotation of the first three principal components (Table 81) from the ecological correlations on the BL diameters of UM1 and UM2, the frequency of cde, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
BL of UM1	−0.63	0.08	0.46
BL of UM2	−0.14	0.14	0.93[†]
Rhesus system (cde)	0.92*	−0.19	0.08
Hunting-gathering	0.01	0.90***	0.19
Cattle breeding	0.40	−0.83***	0.23
Milking	0.87[†]	−0.13	−0.24
Agriculture	0.15	−0.85**	−0.21

[a] The cumulative proportion of the three principal components is 82.76%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 83. Principal component analysis of the ecological correlations on shoveling of UI1, the frequency of cDE, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Shoveling	−0.41	0.73	0.30	79.32
Rhesus system (cDE)	−0.70	0.38	0.30	73.19
Hunting-gathering	−0.72	−0.57	0.21	88.67
Cattle breeding	0.91	0.14	−0.11	86.58
Milking	0.54	−0.54	0.62[†]	96.78
Agriculture	0.79	0.41	0.31	89.40
Total contribution (%)	49.05	24.65	11.95	85.66
Cumulative proportion (%)	49.05	73.71	85.66	85.66

[a] The number of populations used is 15. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 84. Solution obtained through the normal varimax rotation of the first three principal components (Table 83) from the ecological correlations on shoveling of UI1, the frequency of cDE, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
Shoveling	0.09	0.86	−0.20
Rhesus system (cDE)	−0.36	0.76	−0.15
Hunting-gathering	−0.92	0.06	0.17
Cattle breeding	0.82	−0.40	0.17
Milking	0.10	−0.30	0.93
Agriculture	0.87	0.07	0.36

[a] The cumulative proportion of the three principal components is 85.66%.
[†] $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 85. Principal component analysis of the ecological correlations on shoveling of UI1, the frequency of LAA, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Shoveling	0.74	0.49	−0.35	92.19
Lactase activity (LAA)	−0.69	−0.65	0.07	90.63
Hunting-gathering	0.29	−0.80	−0.11	73.87
Cattle breeding	−0.77	0.41	−0.18	80.16
Milking	−0.71	0.04	−0.60	86.59
Agriculture	−0.47	0.50	0.47	68.88
Total contribution (%)	40.73	28.79	12.54	82.05
Cumulative proportion (%)	40.73	69.52	82.05	82.05

[a] The number of populations used is 10. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
$^{\dagger}p<0.10$; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$, by a two-tailed bootstrap test.

Table 86. Solution obtained through the normal varimax rotation of the first three principal components (Table 85) from the ecological correlations on shoveling of UI1, the frequency of LAA, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
Shoveling	0.94	−0.14	0.10
Lactase activity (LAA)	−0.90	−0.14	−0.27
Hunting-gathering	−0.29	−0.78	0.23
Cattle breeding	−0.17	0.56	−0.68
Milking	−0.21	0.04	−0.91†
Agriculture	−0.17	0.81	−0.01

[a] The cumulative proportion of the three principal components is 82.05%.
$^{\dagger}p<0.10$; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$, by a two-tailed bootstrap test.

Table 87. Principal component analysis of the ecological correlations on the Carabelli trait of UM1, the frequency of Jk*a, and the ways of life.[a]

Variable	Factor loadings			Total variance (%)
	PC I	II	III	
Carabelli trait	0.96**	0.10	0.21	96.47
Kidd system (Jk*a)	0.90**	0.00	−0.14	83.71
Hunting-gathering	0.63†	−0.56†	0.18	74.70
Cattle breeding	−0.06	0.83	−0.35	82.37
Milking	0.68	0.56	−0.17	81.17
Agriculture	−0.12	0.60	0.78†	99.23
Total contribution (%)	43.53	28.39	14.36	86.28
Cumulative proportion (%)	43.53	71.92	86.28	86.28

[a] The number of populations used is 12. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
$^{\dagger}p<0.10$; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$, by a two-tailed bootstrap test.

Table 88. Solution obtained through the normal varimax rotation of the first three principal components (Table 87) from the ecological correlations on the Carabelli trait of UM1, the frequency of Jk*a, and the ways of life.[a]

Variable	Factor loadings		
	Fac I	II	III
Carabelli trait	0.95**	−0.20	0.15
Kidd system (Jk*a)	0.89*	−0.10	−0.20
Hunting-gathering	0.50	−0.69**	−0.17
Cattle breeding	0.12	0.89†	0.10
Milking	0.79†	0.44	0.06
Agriculture	−0.01	0.15	0.98*

[a] The cumulative proportion of the three principal components is 86.28%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Table 89. Principal component analysis of the ecological correlations on the Carabelli trait of UM1, the frequency of T, and the ways of life.[a]

Variable	Factor loadings				Total variance (%)
	PC I	II	III	IV	
Carabelli trait	0.38	0.80	−0.17	0.38	95.59
PTC (T)	−0.54	−0.13	0.79†	0.22	97.86
Hunting-gathering	−0.70	0.58	−0.01	−0.07	82.52
Cattle breeding	0.81	−0.17	0.14	−0.42	88.77
Milking	0.48	0.60	0.50	−0.34	95.16
Agriculture	0.70	−0.17	0.19	0.62*	93.23
Total contribution (%)	38.38	23.42	15.86	14.53	92.19
Cumulative proportion (%)	38.38	61.80	77.66	92.19	92.19

[a] The number of populations used is 15. The number of the principal components shown here was so determined that the cumulative proportion of the variances of principal components exceeded 80%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-ailed bootstrap test.

Table 90. Solution obtained through the normal varimax rotation of the first four principal components (Table 89) from the ecological correlations on the Carabelli trait of UM1, the frequency of T, and the ways of life.[a]

Variable	Factor loadings			
	Fac I	II	III	IV
Carabelli trait	−0.94*	0.19	−0.19	0.02
PTC (T)	0.18	−0.03	0.97†	−0.09
Hunting-gathering	−0.27	−0.09	0.25	−0.83***
Cattle breeding	0.23	0.65†	−0.39	0.51
Milking	−0.31	0.92†	0.06	−0.02
Agriculture	−0.34	0.03	0.08	0.90***

[a] The cumulative proportion of the four principal components is 92.19%.
† $p<0.10$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$, by a two-tailed bootstrap test.

Cephalic index and allele 1 of phosphoglucomutase 1

It is widely known that head shape is strongly associated with temperature (Beals, 1972; Guglielmino-Matessi *et al.*, 1979; Mizoguchi, 1985). But the common variant types of phosphoglucomutase, which catalyzes the interconversion of glucose-1-phosphate and glucose-6-phosphate, have been said not to be associated with any marked functional differences which may be of selective significance (Harris, 1970).

In the present study (Table 21), however, the first principal component (PC I) which is significantly correlated with cephalic index is inversely correlated with allele 1 of phosphoglucomutase 1, average annual temperature, average temperature in the hottest month, average temperature in the coldest month, and the amount of annual rainfall. This may be interpreted as follows: Cephalic index and phosphoglucomutase 1 constitute a character complex, and the complex is significantly associated with annual temperature and rainfall. If so, these significant ecological associations are possibly not due to genetic drift but to adaptation or gene flow, as was argued above.

Cephalic index and colorblindness

Since a report in 1962 by R.H. Post, it became accepted that the frequency of colorblindness is higher in population which started agriculture in earlier times (Hoshi, 1977; Molnar, 1992). This has been explained in general by a hypothesis that color blindness in males is selectively disadvantageous in hunter-gatherers, but with the coming of agriculture and a civilization, the negative selection was relaxed. But Harrison *et al.* (1977) questioned whether mutation pressure could have produced such a large increase of its gene frequency in a period of less than 10,000 years.

In the present study, colorblindness was significantly correlated with cephalic index in the first-step analysis (Table 2). In the second (Tables 5 and 6) and final (Tables 23, 24, 59 and 60) steps, however, no significant tendency was found for these two characters to constitute a character complex. Therefore, nothing can be extracted from these non-significant results.

But, if the relatively high association between cephalic index and colorblindness suggested by Fac III in Table 24 is real, namely, if a short-headed population tends to have a high frequency of colorblindness, then such an association is very interesting because the visual cortex is located in the occipital lobe of the cerebrum. Still, it is not clear how the functional variation of the brain would be involved with the structural variation of the brain case. This is for future research.

Incidentally, although they are not statistically significant, PC I in Table 59 and Fac I in Table 60 suggest that colorblindness is positively associated with cattle breeding and agriculture and negatively with hunting-gathering. If this can be substantiated, it supports the above-mentioned hypothesis on colorblindness and the ways of life.

Nasal index and allele 1 of glyoxalase I

Nasal index was found to be inversely associated with allele 1 of glyoxalase I and latitude, and positively associated with average annual temperature, average temperature in the hottest month, average temperature in the coldest month and the amount of annual rainfall (Tables 25 and 26).

Glyoxalase I (a.k.a. lactoyl-glutathione lyase), together with glyoxalase II, converts methylglyoxal, a toxin produced as a by-product of metabolism, with glutathione into lactic acid (Yasugi *et al.*, 1996). Although it is unknown how this enzyme is involved with the ontogenetic process of forming the shape of the nose, the significant ecological associations found here are, again, possibly not due to genetic drift but to adaptation or gene flow.

Mesiodistal crown diameters of permanent teeth and allele B of the ABO blood group system

It is an accepted fact that the frequency of allele B decreases from Central Asia to western Europe, to the Americas via China and Alaska, and to Australia, and that allele B is virtually not

present in Native Americans nor in Native Australians (Stern, 1960; Dobzhansky, 1963; Mettler and Gregg, 1969; Hoshi, 1977; Lewontin, 1995; Marks, 1995). The lack of allele B in the Americas is generally considered to be a result of the "bottle-neck effect" (Komai, 1966). But Stern (1960) stated that there remained the slight possibility of a gradient in the blood-group alleles reflecting not only gene flow but also unknown selective influences which follow a geographic gradient. Mettler and Gregg (1969) also thought that the differential worldwide distributions in allele frequencies of the ABO blood group system could not completely be explained by random genetic drift because the frequencies in many populations studied were concentrated within one fifth of the possible range for the frequencies. Further, various bacteria have antigens on their cell walls which resemble human ABO antigens (Harrison *et al.*, 1977; Lewontin, 1995). They may have played a role in selection of certain alleles of the ABO system, though the evidence is often ambiguous (Harrison *et al.*, 1977).

In the present study, it was found that the MD crown diameters of UI1, UM1 and UM2 had significant inverse associations with allele B of the ABO system (Tables 9 and 11). But the associations of this character complex with climatic variables or the ways of life were not significant (Tables 29, 30, 39, 40, 65, 66, 75 and 76).

What is interesting here is the fact that allele B is hardly observed in those people whose teeth are very large, such as Native Americans and Native Australians (Matsumura, 1995). As was stated above, the lack of allele B in the Americas has previously been explained by random genetic drift in general. But, as suggested by Stern (1960), the significant among-group associations found in the present study support another explanation for this lack of allele B in the Americas or Australia (Table 1) because dental size seems not to be affected so much by genetic drift.

Mesiodistal crown diameters of maxillary molars and allele 1 of haptoglobin-alpha

In the second-step analyses (Tables 11 and 12), the MD crown diameters of UM1 and UM2 were found to constitute a character complex together with many biochemical/physiological characters, i.e., allele 1 of haptoglobin-alpha (HPA*1 or HP*1), allele S of properdin factor B glycine-rich beta-glycoprotein, allele Se of the ABH secretion, and allele B of the ABO system. In the final-step analyses, it was confirmed that three of these four alleles, i.e., allele 1 of haptoglobin-alpha (the second rotated factor [Fac II] in Table 34), allele S of properdin factor B glycine-rich beta-glycoprotein (PC II in Table 35) and allele B of the ABO system (PC II in Table 39 and Fac II in Table 40), each constituted a character complex together with the MD diameters of UM1 and UM2. Among them, however, only one character complex, consisting of haptoglobin-alpha allele 1 and the maxillary molar MD diameter(s), was found to be associated with a climatic factor, i.e., average temperature in the coldest month (Fac II in Table 34).

As for HP*1, Piazza *et al.* (1981) have reported that it has a relatively high inverse correlation with latitude, and Cavalli-Sforza *et al.* (1994) have shown that it has a relatively high positive correlation with humidity/rainfall. Further, it has been said that haptoglobin may have some association with malaria (a.k.a. "swamp fever") due to the relatively high frequency of HP 1-1 individuals (homozygous for HP*1) in areas having high rates of hemolysis due to malaria, such as Africa (Hoshi, 1977; Harrison *et al.*, 1977). However, in contrast, it is also known that the frequencies of HP*1 are conspicuously low in parts of Asia where such hemolysis is equally common (Harrison *et al.*, 1977).

The present finding that the frequency of HP*1 tends to be high in hot regions (Fac II in Table 34) is consistent with the report listed above on latitude by Piazza *et al.* (1981) and, partly, with the description on malaria by Hoshi (1977) and Harrison *et al.* (1977). But the relation of HP*1 with average temperature in the coldest month shown in the present analysis is not as strong and the association with latitude is not significant (Fac II in Table 34). Therefore, the associations

of HP*1 with latitude, temperature, humidity/rainfall and malaria should be examined in more depth in the future.

But, in any case, the significant association between the maxillary molar MD dimensions and haptoglobin is a new finding. It is, again, a future task to examine whether this among-group association is due to adaptation to the same environmental factors, due to gene flow, or due to some other factors.

Buccolingual crown diameter of the maxillary second molar and alleles MS of the MNS system

The BL diameters of UM1 and UM2 did not show any significant associations with biochemical/physiological characters in the second-step analyses (Tables 13 and 14). However, in the final-step analysis, one character complex was found. This complex is composed of the BL diameter of UM2 and alleles MS of the MNS system, and is significantly associated with the average annual temperature, average temperature in the hottest month, average temperature in the coldest month and the amount of annual rainfall (PC I in Table 43).

According to Molnar (1992), it has been reported that the frequency of type N is higher in persons with rheumatic diseases, though the cause for this is not known. Furthermore, a study by B. Glass conducted in the 1950s found a significant shift in the frequency of the M allele from the old to the young group in the Dunker isolate in Pennsylvania. Glass considered the shift to be the result of genetic drift (Stern, 1960). But, of course, this is not a worldwide phenomenon. The present findings based on worldwide data are, again, possibly not due to genetic drift but to adaptation to the same environmental factors such as temperature and rainfall or due to gene flow.

Shoveling and haplotype cDE of the Rhesus system

UI1 shoveling was found to be significantly associated with alleles cDE of the Rhesus system in the second-step analysis (Fac II in Table 16). But, in the final-step analysis, this character complex was not significantly associated with any natural or cultural environmental variables (Tables 47, 48, 83 and 84).

It has been reported, however, that UI1 and/or UI2 shoveling has significant positive correlations with latitude and significant inverse correlations with temperature (Mizoguchi, 1985), and, similarly, that RH*cDE has a relatively high positive correlation with latitude (Piazza *et al.*, 1981) and a strong inverse correlation with temperature (Cavalli-Sforza *et al.*, 1994).

Therefore, there remains a possibility that the ecological association between these two characters is again not due to genetic drift but to adaptation to the same environmental factors such as temperature or due to gene flow.

Shoveling and lactase activity

Lactase activity had a significant inverse correlation with shoveling in the first-step analysis (Table 2). Furthermore, this character complex seems to be present in both second-step (PC I in Table 15 and Fac I in Table 16) and final-step (PC II in Table 49, Fac II in Table 50, PC I in Table 85, and Fac I in Table 86) analyses although their statistical significance is not certain. Strictly speaking, therefore, it is unclear whether or not this character complex has any associations with natural and/or cultural environmental factors.

As is widely known, lactase activity remains high even in adults in Europe and a few other places where there is a history of rearing cattle or dairying (Dobzhansky *et al.*, 1977; Jones, 1992; Marks, 1995). This is considered in general to be the result of adaptation to milk-use (Dobzhansky *et al.*, 1977; Molnar, 1992). In turn, Boaz and Almquist (1997) believe that lactose intolerance that exists in most of modern humans may be an adaptation that prevents adults, who can eat other foods than milk, from directly competing with their young for nourishment.

Nei and Saitou (1986), however, while taking into account the degree of worldwide variation in the frequency of lactose absorbers and some dis-

cordance in geographical variation patterns between lactose tolerance and the way of life, had a different hypothesis. They assert as follows. Allele PLA^+, used by Nei and Saitou for convenience's sake to denote a dominant gene that keeps the level of lactase high even after weaning, occurred as a mutation from PLA^-, which is an allelic gene of PLA^+ and turns off the production of lactase at the time of weaning, more than 100,000 years ago in the human lineage. Furthermore, PLA^+ seemed to have reached at least some appreciable frequency before the divergence of the three major "races." Although it is not clear whether the increase in the frequency of PLA^+ was due to some type of selection or genetic drift, the increase during this period was almost certainly unrelated to milk consumption.

On the other hand, the fact remains that the frequency of lactose absorbers varies from 0 to 46% across the Pacific (Cheer *et al.*, 2000). Cheer *et al.* reported, on the basis of pedigree data of 58 adult Tokelauans (Polynesians) whose lactose digestion capacities had been measured, that the high frequency of lactose-absorbing individuals is most likely due to the contribution of European genetic material to the Tokelau population following massive depopulation after the Peruvian slave raids of 1863. They maintain that this finding is clear evidence for the role of a population bottleneck followed by gene flow and genetic drift.

Although they are not statistically significant, the factor loadings on PC I in Table 85 suggest that shoveling, a character probably controlled by polygenes, is inversely associated not only with lactase activity but also with cattle breeding and milking. If this is the case, these ecological associations based on the worldwide data are, again, possibly not due to genetic drift but to adaptation to an environmental factor such as the way of life or due to gene flow.

*Carabelli trait and allele Jk*a of the Kidd system*

It has been suggested that the UM1 Carabelli trait is strongly associated positively with the subsistence technique of milking and inversely with mean relative annual humidity and the amount of annual rainfall (Mizoguchi, 1993a). In the present analyses, it was found that the Carabelli trait was significantly associated with allele Jk*a of the Kidd system (PC I in Table 87 and Fac I in Table 88). Furthermore, using a 10% significance level, both the associations of this character complex with milking and with hunting-gathering were found to be significant (PC I in Table 87 and Fac I in Table 88). As suggested by PC II in Table 87 and Fac II in Table 88, it appears in general that hunting-gathering is inversely associated with cattle breeding or milking. But, PC I (Table 87) and Fac I (Table 88) are independent of PC II (Table 87) and Fac II (Table 88), respectively. Therefore, if the associations shown by PC I (Table 87) and Fac I (Table 88) are real, these imply that hunter-gatherers with the milking subsistence technique tend to have relatively-well-developed Carabelli cusps and allele Jk*a at relatively high rates.

Although the role of allele Jk*a of the Kidd system remains to be specified in the ontogenetic process of forming a Carabelli cusp, the strong association between these two characters is possibly not due to genetic drift but to adaptation to shared unknown environmental factors or due to gene flow.

Summary and Conclusions

In order to search for concrete determinants for morphological characters, ecological or between-group correlations were estimated among 10 morphological characters, 37 genes for biochemical/physiological characters, 6 climatic variables and 4 ways of life by using worldwide data. The principal component analyses and the rotation of their results on these variables suggested that there were many strong ecological associations between some morphological characters and some genes for biochemical/physiological characters.

Among these, remarkable findings are as follows. Cephalic index is inversely associated not only with allele 1 of phosphoglucomutase 1 but

also with annual temperature and rainfall. Nasal index is inversely associated with allele 1 of glyoxalase I and positively with annual temperature and rainfall. The MD crown diameters of UI1, UM1 and UM2 have inverse associations with allele B of the ABO system. The MD crown diameter of UMI is positively associated with haptoglobin-alpha allele 1 and average temperature in the coldest month. The BL diameter of UM2 is inversely associated with alleles MS of the MNS system and positively with annual temperature and rainfall. UI1 shoveling is positively associated with alleles cDE of the Rhesus system. Finally, the Carabelli trait is positively associated with allele Jk*a of the Kidd system.

Although an ecological correlation between a monogenic/oligogenic character and an environmental factor may be caused by genetic drift, that between a polygenic character and an environmental factor or between a polygenic character and another character of any kind seems unlikely to be affected by genetic drift. In the latter case, the ecological correlation is inferred to be due to adaptation to the same environmental factors or due to gene flow. Most of the significant associations found here between morphological characters and alleles for biochemical/physiological characters are, therefore, considered possibly to be caused by adaptation to the same environmental factors or by gene flow.

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