# Developmental homeostasis and heterozygosity for blood group loci in a human population

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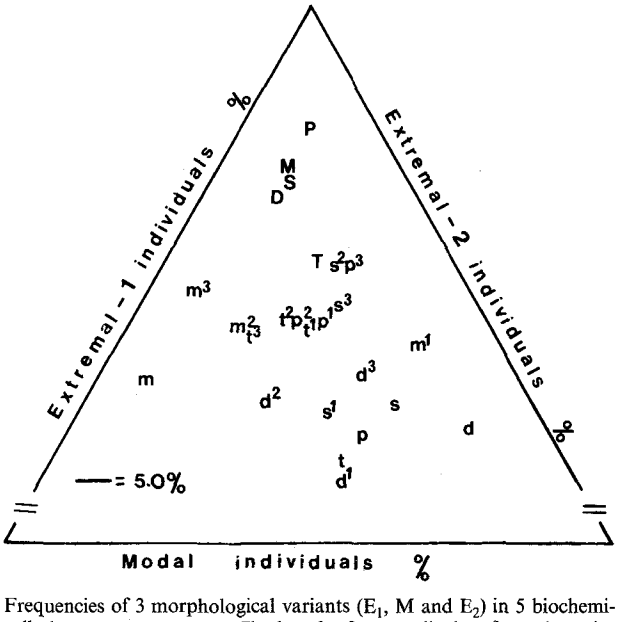
*Summary.* Relationship between the variability of 5 independent morphological characters and the heterozygosity level at 4 blood group loci were determined in Israel. An increase in the heterozygosity level led to a reduction of the range and coefficient of variation of the morphological traits and also led to an increase of modal phenotype frequencies in the group.

That a single gene can affect development of various phenotypical traits (pleiotropy) is well known. As Mayr[2,3] noted, each gene has numerous pleiotropic manifestations which can increase or diminish the biological adaptability of the phenotype. From the aspect of stabilizing selection under constant environmental conditions, the average phenotype will be characterized by maximal fitness[4,5]. The capability of an organism to develop an average phenotype under a relatively wide range of environmental conditions, is designated developmental homeostasis[6-8]. Lerner[6] was among the first to formulate the concept of developmental homeostasis, whereby an increase in heterozygosity would lead to reduction of phenotypic variability and would favor the trend towards the average in the phenotype. Other recent studies have shown that in comparisons of homozygous and heterozygous individuals in a single population for 1 enzymatic locus, morphological variability of the heterozygotes tended to be less than that of the homozygous group[9,10]. Negative correlation between the extent of biochemical heterozygosity and morphological variability was found also in studies of a number of populations within the same animal species (e.g. marine molluscs[8], and lizards[7]). Yet equivalent data for human populations are almost non-existent [11], and we have not found in the literature any data on correlations in man between the degree of individual heterozygosity and the variability of morphological traits. The present study was therefore intended to ascertain whether significant differences in morphological characters exist between biochemically homozygous and heterozygous individuals in human populations and if affirmative, whether any increase in the individual heterozygosity level in the group is accompanied by a decrease in morphological variability.

To this end, 201 healthy Jewish Israeli males aged 18–22 were sampled. We chose only those individuals both parents of whom were Ashkenazi Jews from Europe. 'Askenazi Jews are essentially one uniform and homogeneous group with respect to all genetic markers in the blood[12,13]. Since the observed frequencies of genotypes for 7 selected loci (Phosphoglucomutase-1, Alkaline phosphatase, Adenylate kinase and the 4 blood-group loci MN, Ss, Cc (Rhesus system) and Duffy were in good agreement with those expected according to the Hardy-Weinberg equation, we concluded that our group represented a sample from a single panmictic population. 48 morphological traits[15] were also considered in these individuals and were subjected to principal component analysis[14]. The distribution of each trait was evaluated in comparison to a 'normal' curve and any asymmetrical distributions were normalized by $\log_e X$ transformation. Individuals were designated as hetero-




Frequencies of 3 morphological variants ($E_1$, M and $E_2$) in 5 biochemically heterozygous groups. The length of perpendiculars from the point to the base of the triangle and to its left and right sides are the frequencies of M, $E_1$ and $E_2$ individuals, respectively. The capital letters designate the tetraheterozygous group, the small letters with numerals designate heterozygous groups at 1, 2 or 3 loci according to the numeral, and the small letters without numerals represent the homozygous group.

Table 1. Fiducial levels of differences in frequencies of $E_1$, M and $E_2$ variants between 5 heterozygous groups ($\chi^2$-test) I, and between completely homozygous and tetraheterozygous groups (t-test) II. Coefficients of correlation; r, between levels of heterozygosity and percentage of modal individuals in 5 heterozygous groups. (The frequencies and percentages were subjected to arc-sinus transformation before calculation of correlation coefficients.)

| Statistical parameters | Traits S | T | M | D | P |
|---|---|---|---|---|---|
| I | 0.159 | 0.671 | 0.549 | 0.054 | 0.434 |
| II | 0.061 | 0.120 | 0.107 | 0.089 | 0.050 |
| r | 0.908 | 0.860 | 0.943 | 0.833 | 0.950 |
| p | 0.03 | 0.06 | 0.02 | 0.08 | 0.01 |

Table 2. Main statistical parameters; A, of morphological trait distributions in absolute values; B, of $E_1$, M, $E_2$ individuals frequency distributions in heterozygous groups 0 and 4

| Traits and sample size | Statistical parameters | A Homozygotes | A Heterozygotes | B Homozygotes | B Heterozygotes |
|---|---|---|---|---|---|
| Stature | Range | 160.4–192.8 | 162.7–179.9 | – | – |
| N = 19 vs 11 | CV | 4.60 | 3.06 | 35.62 | 28.25 |
| | K | −0.13 | 0.02 | −1.21 | 1.86 |
| Bi-trochanteric diameter | Range | 26.3–34.8 | 27.4–33.8 | – | – |
| N = 18 vs 10 | CV | 8.71 | 6.54 | 42.45 | 33.33 |
| | K | −1.28 | −0.36 | −1.73 | 0.08 |
| Mesosternal chest* | Range | 6.70–6.90 | 6.70–6.90 | – | – |
| N = 19 vs 11 | CV | 0.78 | 0.76 | 40.08 | 28.25 |
| | K | −0.30 | 1.19 | −0.31 | 1.86 |
| Digit length | Range | 6.5–8.2 | 6.6–7.7 | – | – |
| N = 15 vs 10 | CV | 6.72 | 4.71 | 30.70 | 29.88 |
| | K | −1.02 | 0.24 | −0.47 | 1.50 |
| Palm length | Range | 9.6–12.0 | 9.6–12.0 | – | – |
| N = 19 vs 10 | CV | 6.32 | 5.71 | 39.43 | 23.57 |
| | K | −0.93 | 1.96 | −1.52 | 4.50 |

* $-\log_e X$ transformed traits.

zygotes 0, 1, 2, 3, 4, 5, etc. in accordance with the level of biochemical heterozygosity, the numerals referring to the numbers of loci in the heterozygous condition in each individual. Since individuals heterozygous for 5 or more loci were not encountered in our sample, we confined ourselves to 4 blood-group loci. The frequency of heterozygotes for these 4 loci were higher than for the remaining 3 enzymatic loci.

Individuals were divided by morphological characters into 3 categories, namely, modal category M ( = average ± 0.67 S.D.) extreme category 1 ($E_1$‹M) and extreme category 2 ($E_2$›M). The frequencies of $E_1$, M and $E_2$ individuals were calculated in each heterozygous group. The main statistical parameters (mean, coefficient of variation and kurtosis) of morphological trait distributions in each heterozygous group were also calculated. Coefficient of variation and kurtosis were also calculated for the frequency distribution of $E_1$, M and $E_2$ individuals in each heterozygous group. Of the studied 48 morphological characters, 17 showed trend differences in various heterozygous groups. In the present paper we concentrate on the 5 traits Stature(S), Bi-Trochanteric diameter (T), Mesosternal Chest Circumference (M), Digit length of 2 (D) and Palm length (P) which were separated by principal component alalysis as independent variables.

The frequencies of $E_1$, M and $E_2$ individuals in 5 heterozygous groups for morphometric traits are given in figure 1. It is evident that for all the evaluated traits, maximal frequency of M individuals was in tetraheterozygotes and minimal – in completely homozygous group. Differences between the 5 heterozygous groups, however, were not significant (table 1). As for the 2 extreme groups 0 and 4 there was a significant difference only for P, but combined probability of significance[16] for the 5 independent t-tests was ‹0.01. Moreover, coefficients of correlation between the level of heterozygosity and the frequency of modal individuals in the group were extremely high and in 3 cases also statistically significant (table 1). As can be seen from table 2 the range of the character values in the tetraheterozygous group (4) tend to be narrow, the CV values lower and the kurtosis higher than in the homozygous group (0). These differences are very evident when we compare the frequency distributions of the $E_1$, M and $E_2$ individuals (table 2). Here the kurtosis for each trait in the homozygous group has a negative value, indicating a paucity of M individuals, whereas in the heterozygous group the kurtosis is positive, indicating an excess of M individuals.

In summary, our data show that in human populations the variability of some morphological traits is related to the biochemical heterozygosity level and that an increase in heterozygosity may clearly lead to a decrease in morphological variability-'developmental homeostasis' and will also favor the average phenotype.

1 We are very grateful to Professor B. Arensburg of our department at the Tel Aviv University for his kind permission to use anthropometric data collected by him.

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0014-4754/84/070748-02$1.50 + 0.20/0


## Supernumerary (B) chromosome in *Anopheles indefinitus* (Diptera, Culicidae)[1]

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*Summary.* Larval brain mitotic karyotype of *An. indefinitus* from Kanchanaburi exhibits a supernumerary (B) chromosome which is apparently common in that population. 1 or 2 B-chromosomes have been observed in the samples from 5 isofemale lines examined.

The karyotype of eukaryotes is essentially invariable with respect to chromosome number. Yet, the genome of many species of plants and animals comprises extra heterochromatic elements called supernumerary or B-chromosomes. These may be of various sizes, shapes and number[2,3]. The B-chromosome, however, does not follow strictly the law of Mendelian segregation. Although B-chromosomes are widespread among insects in general, they are apparently rare in the order Diptera, particularly in anophelines. There are only 2 reported cases of *Anopheles* species (i.e. *An. maculipennis* and *An. messae*) showing B-chromosomes[4]. We report here the occurrence of a B-chromosome in *An. indefinitus* collected in Thailand. It was discovered during the course of metaphase karyotype analysis of anopheline mosquitoes in Southeast Asia.

*Materials and method.* Samples from natural populations of *An. indefinitus* were obtained during a mosquito collection made in August 1982, in the Srinakarin Dam area, Kanchanaburi Province, some 180 km west of Bangkok, Thailand. 5 wild-caught females of *An. indefinitus* were captured and given a full bloodmeal. Each isofemale line was set up to obtain $F_1$ larvae under laboratory conditions. The brain ganglia of the early 4th-stage $F_1$ larvae were used for mitotic chromosome study after pretreatment with a 0.1% colchicine solution. A modified method of Baimai[5] was used for air-dried metaphase