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Segregation Analysis of Some Anthroposcopic Traits: I. Binary Traits with Age-Independent Penetrance

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Abstract – Genetic analysis of a number of anthroposcopic traits was attempted using a sample of pedigrees from the Kirgiz population. We used methods of binary trait segregation analysis, which allowed us to analyze pedigrees of arbitrary structure. The genetic model applied was based on the monogenic diallelic mode of inheritance with arbitrary genotype penetrances and allowed for different phenotypic expressions of a genotype in males and females. The hypothesis of monogenic diallelic inheritance could not be rejected for the following 12 traits: ability to roll the tongue, earlobe, auricular tubercle, nose shape, base of the nose, accreted eyebrows, fold of the upper eyelid, margin of the auricle, vertex hair whorl, cheekbones, cheek dimples, and height of the nose bridge. Sex dimorphism was demonstrated for the latter five traits. Problems of the relationship between sample informativeness and precision of parameter estimation are discussed.

INTRODUCTION

The study of the genetic control of anthroposcopic traits is interesting for two reasons. First, data on inheritance of these traits add to knowledge of individual human genetics. Second, researchers may use relatively inexpensive specific chromosomal markers.

The exact mode of inheritance of the studied traits is unknown. Cheek dimples are thought to be inherited as a dominant trait with incomplete penetrance [1, 2]. As for the earlobe, evidence exists in favor of the dominant inheritance of a free earlobe [2], but some authors suggest that this trait has polygenic inheritance [3, 4]. Data on inheritance of the capability to roll the tongue are contradictory. Sturtevant [5] considers the trait to have dominant control. However, Matlock [6] found high discordance for this trait among monozygotic twins. This suggests low heritability for this trait. A hypothesis exists that a cape-shaped hair border is under dominant control [7]. Bernstein [8] showed that the direction of vertex hair whorl curling is genetically determined and demonstrated that clockwise curling prevails.

We report the results of segregation analysis of some anthroposcopic traits and attempt to describe their inheritance in terms of a monogenic diallelic model.

MATERIALS

Data were collected in 1990 - 1992 in Kirgizia. We investigated Kirgiz families, selected with respect to probands in the course of the Atherosclerosis program. Probands were males who had a myocardial infarction (MI) in any form (macrofocal, microfocal, or

transmural) or suffered from angina of effort before 50 years of age. Information on probands was obtained from the coronary heart disease (CHD) registry in Bishkek, Kirgizia. We also included in the sample some families of probands who died before the investigation began. Of the investigated probands, 93% lived in Bishkek and 7% lived in Issyk-Kul'skaya oblast'. The sample included all members of the proband pedigree who were available for investigation. This availability was the only restriction on pedigree sampling.

The sample consisted of (1) 49 nuclear families, including 13, 22, 9, and 5 families with one, two, three, and four offsprings, respectively, and (2) a number of families with more complex structure, including 6, 18, 1, and 1 families with 7 or less, 8 - 15, 22, and 23 members investigated, respectively. Thus, the total sample comprised 447 persons.

We determined 24 anthroposcopic traits for every member of a pedigree. They were estimated by a scale using corresponding schemes and scales. All specialists who performed estimation had gone through standardization in anthropological measurements. The methods of estimation are described in detail elsewhere [9].

Here, we analyze inheritance of 12 traits, for which the phenotypic manifestations are presented in Table 1.

METHODS

We performed segregation analysis using MAN-A2 software (a revised version of MAN-A1 [10]).

We assume that a trait is determined by one diallelic gene A ; genotypes A_1A_1 , A_1A_2 , and A_2A_2 are denoted by numbers $g = 1, 2$, and 3 , respectively. We may assume that the population frequencies of genotypes $p_g = p_1, p_2, p_3$.

Table 1. Phenotypic characteristics of binary traits

Trait	Phenotype 0	Phenotype 1
Cheek dimples	Yes	No
Margin of auricle (folded edge of floor of the auricle)	Slightly marked	Moderately or strongly marked
Ear lobe	Pendant or intermediate	Attached
Auricular tubercle (a tubercle on the ear edge, at the border of the upper and the lower parts)	Marked	Not marked
Direction of vertex hair whorl curling	Clockwise	Counter-clockwise
Accreted eyebrows	Strongly or moderately marked	Not marked
Fold of the upper eyelid (a transverse fold of the eyelid just below the supraoptical sulcus)	Marked	Moderate or not marked
Height of the nose bridge	High or intermediate	Low
Base of the nose	Elevated or intermediate	Lowered
Nose shape	Concave or straight	Convex
Tongue rolling	Able	Unable
Cheekbones	Marked	Intermediate or not marked

and p_3 , are in equilibrium: p^2 , $2pq$, and q^2 respectively, where p is the population frequency of allele A_1 , and $q = 1 - p$.

Gene transmission from parents to offspring is described by transmission probabilities: $\tau_g = P(A_1/g)$ is the probability that an individual with genotype g will produce a gamete with allele A_1 . Under normal Mendelian segregation, $\tau_g = 1.0$, 0.5 , and 0.0 for $g = 1, 2$, and 3 , respectively. We analyze a qualitative binary trait, arbitrarily denoting the norm as $x = 0$ and an abnormality as $x = 1$.

Correspondence of phenotype to genotype is determined by the probability $f(x/g)$, i.e., the probability that an individual with genotype g has trait x . For a binary trait, $f(1/g)$ is the penetrance of genotype g ; in this case, $f(0/g) = 1 - f(1/g)$. One may suppose penetrances for different sexes to be unequal: $f_{\text{mal}}(1/g) = W_g$ and $f_{\text{fem}}(1/g) = V_g$.

Although the pedigrees were ascertained using a proband, we considered it possible to neglect this fact, assuming that the anthroposcopic traits studied were not associated with MI or CHD. Therefore, we did not perform a correction of the likelihood function for the method of pedigree selection.

The testing criteria for the hypothesis on the mode of trait inheritance were routine. They represented variants of the likelihood ratio test. Let $P_i(\hat{\alpha}_1, \dots, \hat{\alpha}_m)$ be the probability for a random pedigree to be of i type, provided the monogenic model with m parameters is

true and $\hat{\alpha}_i$ are the maximum likelihood estimates of the parameters. Suppose $P_i(\hat{\alpha}_1, \dots, \hat{\alpha}_k, \hat{\alpha}_{k+1}, \dots, \hat{\alpha}_m)$ is the same probability if the first k parameters are estimated and values for the remaining $(m - k)$ parameters are known *a priori* (such parameters are indicated by asterisks in tables below). Then

$$2 \left(\sum n_i \ln \frac{P_i(\hat{\alpha}_1, \dots, \hat{\alpha}_m)}{P_i(\hat{\alpha}_1, \dots, \hat{\alpha}_k, \alpha_{k+1}, \dots, \hat{\alpha}_m)} \right) = 2(LH_1 - LH_2),$$

where LH is the maximum of the likelihood function. LH follows an asymptotic χ^2 distribution with the number of degrees of freedom $df = m - k$ [11]. On this basis, we tested the main genetic hypotheses – an assumption about the gene determination of a trait and a hypothesis about the Mendelian segregation of the alleles – as well as the hypothesis about the sex dimorphism of the phenotypic expression of genotypes.

Fitting of the monogenic hypothesis to the data obtained was tested using a combined test [12]. For the hypothesis to be approved, the following conditions had to be met: (a) the hypothesis of absence of genetic control of the trait had to be rejected (this was achieved via an assumption that the Elston–Stewart transmission probabilities τ_g are all identical: $\tau_g = \tau$), and (b) the hypothesis of Mendelian segregation of alleles could not be rejected (estimates of τ_g had to be close to Mendelian values).

RESULTS

Inheritance of Binary Traits with Different Penetrances in Males and Females

Table 2 shows the results of segregation analysis of three traits: margin of auricle (columns 1 - 5), vertex hair whorl (columns 6 - 8), and cheekbones (columns 9 - 11). The maximum likelihood estimates are presented for the following genetic parameters: the frequency, p , of the allele A_1 ; the penetrances, W_g and V_g , for males and females, respectively; the transmission probabilities, τ_g ; and the maximum likelihood value, LH .

All these traits exhibited a substantial sex difference in penetrance; therefore, the results of their analysis are given in one table.

Each column of the table corresponds to a distinct variant of the monogenic model of trait inheritance that was tested.

The first column represents monogenic diallele control of the margin of the auricle with identical genotype penetrances for both sexes. Because the penetrances of the three genotypes are close to those assumed by the intermediate inheritance model, a special assumption is made that $W_1 = 0.0$ and $W_3 = 1.0$ (see column 2). A comparison of the likelihood functions for these two columns shows that this assumption cannot be rejected: the asymptotic value of the likelihood ratio (see Materials and Methods) is $\chi^2 = 1.064$ at $df = 2$. Column 3 represents a similar model; the only difference is that it assumes different penetrance of the heterozygous genotype for males ($W_2 = 0.79$) and females ($V_2 = 0.32$). It is evident that this assumption substantially improved the model: a comparison of columns 2 and 3 gave

$\chi^2 = 16.67$ at $df = 1$. The variances of errors of parameter estimates, m^2 , are given in parentheses. They were obtained using a matrix of second derivatives from the likelihood function. Column 4 represents a model that admits arbitrary values of the transmission probabilities τ_g . As the table shows, their estimates differ insignificantly from the corresponding Mendelian values ($\chi^2 = 0.78$ at $df = 3$). The fifth variant of the model assumes equal transmission probabilities: $\tau_g = \tau$. This is equivalent to a hypothesis about the absence of genetic control of the trait. This assumption was rejected: $\chi^2 = 25.15$ at $df = 2$.

If a number of models that assume different genetic determination of a trait and are controlled by different sets of genetic parameters are statistically indistinguishable (according to the likelihood ratio test), then it is reasonable to choose the simplest model (in terms of its genetic assumptions) as a working model of genetic determination of the trait.

The results of our analysis did not allow us to reject monogenic diallelic determination with different heterozygote penetrances for different sexes and with the frequency of the "normal" allele $p = 0.223 \pm 0.029$. Therefore, the model represented in column 3 of Table 2 could be chosen as a working model of inheritance.

Testing the model with transmission probability estimates τ_g and that with identical values of $\tau_g = \tau$ is necessary for further testing of the monogenic hypothesis. Hereafter, for all traits that can be described by only three variants of the genetic model, we will arrange the model descriptions as follows: (1) a working model (i.e., that accepted on the basis of the analysis performed), (2) a model that uses sample estimates

Table 2. Estimates of model parameters for binary traits with different expression in the sexes

	Margin of auricle ($N = 425$)					Vertex hair whorl ($N = 422$)			Cheekbones ($N = 425$)		
	1	2	3	4	5	6	7	8	9	10	11
p	.155	.269	.223 (.001)	.222	.370	.641 (.012)	.624	.627	.412 (.002)	.452	.367
W_1	.005	.000*	.000*	.000*	.000*	.000*	.000*	.000*	.698 (.002)	.685	.639
W_2	.482	.659	.792 (.006)	.803	1.00	.000 (.016)	.000	.000	W_1	W_1	W_1
W_3	.962	1.00*	1.00*	1.00*	1.00*	1.00*	1.00*	1.00*	1.00*	1.00*	1.00*
V_1	W_1	W_1	.000*	.000*	.000*	.000*	.000*	.000*	.275 (.005)	.255	.183
V_2	W_2	W_2	.321 (.017)	.321	.723	.464 (.058)	.462	.485	V_1	V_1	V_1
V_3	W_3	W_3	1.00*	1.00*	1.00*	1.00*	1.00*	1.00*	1.00*	1.00*	1.00*
τ_1	1.00*	1.00*	1.00*	1.00	.324	1.00*	1.00	.655	1.00*	1.00	.325
τ_2	.500*	.500*	.500*	.430	τ_1	.500*	.551	τ_1	.500*	.347	τ_1
τ_3	.000*	.000*	.000*	.006	τ_1	.000*	.000	τ_1	.000*	.000	τ_1
LH	-189.9	-189.3	-181.0	-180.6	-193.2	-200.1	-199.8	-218.2	-249.4	-248.3	-254.6

* Fixed (given *a priori*) parameter values.

of τ_g , and (3) a model with identical τ_g values. We will restrict the following discussion of models to the presentation of χ^2 test values for comparisons of the first to the second and the second to the third models.

Columns 6 - 8 of Table 2 concern the vertex hair whorl, and their content corresponds to the models described in columns 3 - 5 for the margin of the auricle. Monogenic diallelic control of this trait was not rejected (χ^2 for the difference of columns 6 and 7 was 0.54 at $df = 3$, and for that of columns 7 and 8, $\chi^2 = 36.79$), penetrances in heterozygotes being sex-dependent: males exhibited complete dominance of allele A_1 (clockwise curling), i.e., $W_2 = W_1 = 0.0$, and females exhibited a mode of inheritance close to intermediate ($V_2 = 0.46$).

Taking into account the estimated frequency of A_1 allele $p = 0.641 \pm 0.011$, we can consider that our results confirm the conclusion of Bernstein about the predominance of clockwise curling [8].

Columns 9 - 11 describe the inheritance of the degree of cheekbone expression. When estimating the parameters of the model with different penetrances for all three genotypes, we found that W_1 and W_2 , as well as V_1 and V_2 , had very similar values. Column 9 represents a variant of the model that assumes the dominance of "marked" cheekbones with incomplete penetrance: for males, $W_2 = W_1 = 0.698$, and, for females, $V_2 = V_1 = 0.275$. The value of the χ^2 test for the difference of columns 9 and 10 was 2.34 at $df = 3$, and for that of columns 10 and 11, it was 12.77 at $df = 2$. Thus, in this case, the monogenic hypothesis also cannot be rejected.

Inheritance of Binary Traits with Sex-Independent Penetrances

None of the traits presented in Table 3 showed sex dependence of expression.

The first three columns represent the above "obligate" variant models of inheritance for tongue rolling. When testing the monogenic diallelic model with different probabilities of "abnormal" phenotype manifestation for all three genotypes ($W_1 \neq W_2 \neq W_3$), we found the parameter estimates to be similar to those of the intermediate inheritance model. Therefore, we suggested that $W_1 = 0.0$ and $W_3 = 1.0$, as shown in column 1 of Table 3 (the variances of errors of parameter estimates are given in parentheses). This suggestion could not be rejected: $\chi^2 = 0.45$ at $df = 2$ (data not shown). Comparison of columns 1 and 2 gave $\chi^2 = 0.10$ at $df = 3$, and that of columns 2 and 3 gave $\chi^2 = 20.14$ at $df = 2$. Therefore, the monogenic diallele model with a mode of inheritance close to intermediate ($W_2 = 0.438 \pm 0.100$) and a "normal" phenotype frequency $p = 0.556 \pm 0.041$ is not rejected.

Such a mode of inheritance does not agree with the opinion of some authors [5], who consider this trait to be under dominant control. However, our model could partially explain the high discordance of monozygotic

twins found by Matlock [6]: only half of the heterozygotes are able to roll the tongue.

Columns 4 - 6 represent the inheritance of accreted eyebrows, and their content corresponds to that of columns 1 - 3 for tongue rolling. The monogenic diallele model, with a frequency of abnormal phenotype manifestation in heterozygotes $W_2 = 0.368 \pm 0.092$ and a normal allele frequency $p = 0.552 \pm 0.039$, is not rejected (for the difference of columns 4 and 5, $\chi^2 = 2.17$, and for that of 5 and 6, $\chi^2 = 26.97$).

Columns 7 - 9 represent the results of analysis of the auricular tubercle. Column 7 shows estimated parameters of the model that assumes identical penetrances in both sexes and dominance of allele A_1 , which determines a marked auricular tubercle ($W_2 = W_1$). The error variances of these estimates are given in parentheses. Comparison of the likelihood functions for columns 7 and 8 gives $\chi^2 = 2.65$ at $df = 3$, and for columns 8 and 9, $\chi^2 = 21.32$ at $df = 2$. Therefore, the monogenic hypothesis assuming A_1 dominance with complete penetrance is not rejected, i.e., the auricular tubercle has a recessive inheritance with incomplete penetrance: it is manifested only in individuals with genotype g_3 (A_2A_2), the penetrance being $W_3 = 0.825 \pm 0.044$.

For the ear lobe, a similar hypothesis about dominance of allele A_1 , which determines a free ear lobe but with incomplete penetrance ($W_2 = W_1 \neq 0.0$), is not rejected (columns 10 - 12). For the difference of columns 10 and 11, $\chi^2 = 4.93$ at $df = 3$; for that of columns 11 and 12, $\chi^2 = 39.03$ at $df = 2$.

This does not contradict literature data [2] on the dominant inheritance of the free ear lobe. However, this conclusion does agree with the results of works [3, 4] that assume the polygenic inheritance of this trait, because the polygenic model is known to be "omnivorous," describing a great variety of modes of inheritance.

Columns 13 - 15 correspond to the nose shape. There is evidence that the prevalence of convex nose shapes increases with age and that of concave shapes decreases. Females more frequently have a concave rather than convex nose [13]. In our sample, age dependence and sex differences in penetrance were not statistically significant.

For this trait, the estimated parameters of the model with different penetrances for three genotypes were in good agreement with the assumption of A_2 dominance. This is in contrast to the previous two traits, which exhibited the dominance of allele A_1 . Column 13 gives estimates of parameters of the model assuming dominance of the convex nose shape with incomplete penetrance ($W_2 = W_3 = 0.511$). The error variances of these estimates are given in parentheses. Estimates of τ_g presented in column 14 differ insignificantly from Mendelian values ($\chi^2 = 4.52$ at $df = 3$). The hypothesis of identical τ_g values (column 15) is rejected ($\chi^2 = 26.05$ at $df = 2$).

Columns 16 - 18 represent the inheritance of the nose base form. Evidence exists [13] that the prevalence of an elevated base of the nose decreases with

Table 3. Estimates of model parameters for binary traits with identical expression in the sexes

Tongue rolling (N = 426)				Accreted eyebrows (N = 427)			Auricular tubercle (N = 420)			Ear lobe (N = 425)			Nose shape (N = 425)			Base of the nose (N = 425)		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
P	.556 (.002)	.561	.623	.552 (.002)	.579	.745	.099 (.001)	.148	.347	.459 (.001)	.416	.582	.897 (.0004)	.951	.938	.713 (.002)	.678	.705
W ₁	.000*	.000*	.000*	.000*	.000*	.000*	.000*	.000*	.000*	.180 (.002)	.078	.285	.000*	.000*	.000*	.000	.000	.052
W ₂	.438 (.010)	.431	.536	.368 (.009)	.352	.740	W ₁	W ₁	W ₁	W ₁	W ₁	W ₁	W ₃	W ₃	W ₃	.313 (.011)	.326	.230
W ₃	1.00*	1.00*	1.00*	1.00*	1.00*	1.00*	.825 (.002)	.891	.978	1.00*	1.00*	1.00*	.511 (.0089)	.831	.526	.717 (.048)	.734	.934
τ ₁	1.00*	1.00	.596	1.00*	.954	.706	1.00*	1.00	.288	1.00*	1.00	.529	1.00*	.973	.878	1.00*	1.00	.800
τ ₂	.500*	.478	τ ₁	.500*	.413	τ ₁	.500*	.320	τ ₁	.500*	.342	τ ₁	.500*	.575	τ ₁	.500*	.634	τ ₁
τ ₃	.000*	.000	τ ₁	.000*	.051	τ ₁	.000*	.027	τ ₁	.000*	.097	τ ₁	.000*	.000	τ ₁	.000*	.000	τ ₁
LH	-278.2	-278.1	-288.2	-270.6	-269.5	-283.0	-255.4	-254.1	-264.7	-273.5	-271.0	-290.5	-128.9	-126.7	-139.7	-196.4	-195.6	-202.9

* Fixed parameter values.

age. Sex differences also occur. Among females, elevated bases of the nose are more frequent and lowered ones are less frequent. For our sample from the Kirgiz population, the inheritance model was not significantly improved after sex dimorphism and age dependence were included. Therefore, we restricted the consideration by presenting variants of the model that do not take into account age dependence or sex dimorphism.

Column 16 shows estimates of parameters of the model with different probabilities of an "abnormal" phenotype manifestation for all three genotypes. The monogenic diallelic hypothesis with A_1 allele (nonlowered shape) frequency $p = 0.713 \pm 0.043$ is not rejected (a comparison of columns 16 and 17 gives $\chi^2 = 1.63$ at $df = 3$, and one of columns 17 and 18 gives $\chi^2 = 14.61$ at $df = 2$).

A hypothesis of age-dependent penetrances and a model that did not assume the Hardy-Weinberg equilibrium were tested for all traits represented in Tables 2 and 3. These suggestions did not significantly improve the model of inheritance.

Additional Results

Table 4 shows the results of segregation analysis of three additional traits. We found sex-dependent penetrances for some genotypes of the first two traits, e.g., for A_1A_2 heterozygotes for the bridge height gene and for all three cheek dimple genotypes. For the latter trait, an allele determining the absence of cheek dimples is supposed to be dominant. We did not find sex dimorphism the phenotypic manifestations of the upper eyelid fold. We placed these three traits in a separate table for the following reason. From the formal point of view, the characteristics of inheritance of these traits fit the two basic criteria of the monogenic control hypothesis:

- (1) $\chi^2_{1,2} = 1.22$, $\chi^2_{4,5} = 6.54$, and $\chi^2_{7,8} = 1.24$ at $df = 3$;
 - (2) $\chi^2_{2,3} = 32.30$, $\chi^2_{5,6} = 24.37$, and $\chi^2_{8,9} = 13.24$ at $df = 2$.
- In other words, the hypothesis about Mendelian segre-

gation of alleles is not rejected, and the hypothesis about the absence of genetic control for each of the three genotypes is rejected with a high probability.

However, estimates of the Elston-Stewart transmission probabilities differ, although not significantly, from the corresponding Mendelian values (1.0, 0.5, and 0.0). For the cheek dimples, one might explain the difference between $\tau_2 = 0.776$ and the expected value, 0.5, by lack of a sufficient number of heterozygotes for correct τ_2 estimation, due to a low A_1 allele frequency ($p = 0.12$). However, such an explanation is not true for τ_3 values of the first and third traits studied. The observed deviations of τ_g values from the Mendelian ones are statistically insignificant and are possibly due to a nonrepresentative sample.

As for cheek dimples, note that our model, which assumes different phenotypic expression in different sexes and dominance of the presence of dimples with complete penetrance in females and incomplete penetrance in males, does not contradict the literature data [1, 2].

In addition, we performed segregation analysis of nine more anthroposcopic characteristics. Here, we do not describe the full results of this analysis, but restrict ourselves to the conclusions.

For the traits ability to twist the tongue, hair type, intereye distance, anthelix, and thickness of lips, as well as for those presented in Table 4, the hypothesis of the absence of inheritance is rejected, while Mendelian allele segregation is not rejected. However, estimates of the transmission probabilities τ_g differ from the Mendelian values to a substantially greater extent than τ_g values for the traits from Table 4. Such a result may be due to a nonrepresentative sample for the analysis of these traits.

For the traits tip of the nose, shape of the mouth, and widow's peak (a specific shape of hair border), a hypothesis about the absence of inheritance was rejected, but so was the hypothesis of Mendelian segregation of alleles. Moreover, we found substantial differ-

Table 4. Traits with transmission probabilities (τ_g) deviating from the Mendelian values

Height of the nose bridge ($N = 425$)				Cheek dimples ($N = 425$)			Fold of the upper eyelid ($N = 426$)		
	1	2	3	4	5	6	7	8	9
p	.693	.537	.795	.120	.072	.191	.404	.438	.456
W_1	.000*	.000*	.000*	.286	.352	.372	.000*	.000*	.000*
W_2	.230	.000	.519	W_1	W_1	W_1	W_3	W_3	W_3
W_3	1.00*	1.00*	1.00*	.828	.813	.931	.782	.835	.855
V_1	.000*	.000*	.000*	.000	.000	.000	W_1	W_1	W_1
V_2	.537	.239	.936	V_1	V_1	V_1	W_2	W_2	W_2
V_3	1.00*	1.00*	1.00*	.792	.786	.679	W_3	W_3	W_3
τ_1	1.00*	1.00	.815	1.00*	1.00	.349	1.00*	.956	.499
τ_2	.500*	.482	τ_1	.500*	.776	τ_1	.500*	.476	τ_1
τ_3	.000*	.169	τ_1	.000*	.000	τ_1	.000*	.170	τ_1
LH	-225.7	-225.1	-241.2	-263.7	-260.4	-272.6	-268.9	-268.3	-274.9

* Fixed parameter values.

ences of transmission probability (τ_g) values from the Mendelian values. This suggests possible polygenic control of these traits.

For the trait eyebrow slope, Mendelian segregation was rejected and the hypothesis of absence of inheritance was not rejected. Therefore, it is reasonable to suggest an absence of genetic control of the trait.

DISCUSSION

The method of segregation analysis used in this study is quite routine; we did not introduce substantial modifications as compared to commonly used methods [14]. The sample consisted of 75 pedigrees and, in total, 420 to 427 individuals (depending on the particular trait). Pedigrees with complex structure provided the sample with an informativeness that was sufficient for segregation analysis. Therefore, we consider the results obtained, i.e., monogenic control of traits listed in Table 1, to be quite credible.

It is natural that the result of such a segregation analysis, which used pedigree sampling from the population, is not a final result (this is the case for any analysis of hybrids). The history of genetics exhibits a number of cases in which a single study demonstrated monogenic diallelic control of some trait, whereas further research did not confirm this fact. This is due to a number of reasons, both genetic and methodological. Therefore, a definite type of genetic control of a trait is considered to have been determined in one of the following cases: (1) This type of genetic control was confirmed in several independent investigations. (2) The hypothetical gene was located on the chromosome by recombinational analysis methods, i.e., becomes not a hypothetical but a real gene.

For some of the studied traits, our results partially confirm those already reported. They agree with the conclusions of other authors in an essential aspect, monogenic control, although they disagree in a less important one, estimates of genetic parameters. The latter is quite natural, for every population may have its

own allele frequencies and its own gene pool, which modifies expression of genotypes. For other traits, we failed to find literature data on such segregation analysis and, therefore, we must consider the conclusion about their monogenic control as a preliminary one.

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