

## SIMPLE MODES OF INHERITANCE AND THE STUDY OF TWINS<sup>1</sup>

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Twins, both monozygotic and dizygotic, are of inestimable value in the study of the interaction of heredity and environment in the development of human traits. With the exception of mutations which may occur during the life of the individual, intra-pair variations in monozygotic twins are due to factors other than heredity. Many implications easily follow in the interpretation of experimental data based on the study of twins, not all of which are necessarily true. One such implication is that when intra-pair variation in some trait is greater in dizygotic than in monozygotic twins, such differences are a measure of the extent to which heredity is responsible for the trait. While it is true that the differences between the two types of twins are due largely to heredity, yet it must be remembered that dizygotic twins are as similar in hereditary make-up as brothers and sisters, and thus such comparisons give us only a partial estimate as to the role played by hereditary factors. Comparisons of monozygotic twins with foster sibs or unrelated pairs of individuals reared in orphanages should give a more accurate basis for evaluating the role of heredity. Dizygotic twins and sibs, however, should also be included in such studies. Members of twin pairs are contemporaries, and thus have more similar environments than sib or random pairs with age discrepancies. Moreover, the prenatal environment of twins, due to crowding and possible imbalances of fetal blood supply, is different from that of single born individuals. While such conditions would not affect many genetic traits, such as blood types and skin pigmentation, yet it has been demonstrated that left-handedness and associated traits occur with greater frequencies in both types of twins than in single born individuals. Recent studies of dermatoglyphics (Cummins, Leche, and McClure, 1932; Leche, 1933) have brought

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<sup>1</sup>Genetic Studies of Monozygotic Twins, No. VI.

out evidence that handedness has a genetic basis. As dizygotic twins and sibs have, on the average, the same degree of genetic similarity, comparisons of dizygotic twins with sibs should give us a measure of the part the unusual prenatal environment of twins plays in bringing about intra-pair differences. Differences between monozygotic twins reared together, minus the differences between dizygotic twins and sibs, should give us a much more accurate estimate of the part played by heredity, than comparisons only of the two types of twins.

The erroneous statement is sometimes made (Rosanoff et al., 1937) that although studies of twins are of great value in estimating the relative parts played by heredity and environment in the etiology of various traits, such data tell us absolutely nothing in regard to the *mode* of inheritance. It has recently been shown (Cotterman, 1937) that intra-pair sib comparisons can be used in the determination of whether or not a given trait could be due to single factor inheritance, although not necessarily indicating which phenotype is dominant. Similar methods can be employed in the analysis of data obtained from dizygotic twins, and may also be made to include a single pair of factors with incomplete dominance, sex-linked and sex-influenced factors.

#### A SINGLE PAIR OF FACTORS, WITH AND WITHOUT DOMINANCE

For a single pair of allelomorphs with incomplete dominance, A and a, let us allow p to represent the frequency of gene A, and q the frequency of gene a. Then, in a population which has reached equilibrium,

$$p + q = 1$$

Also

$$p^2 + 2pq + q^2 = 1$$

$p^2$  = frequency of genotype AA  
 $2pq$  = frequency of genotype Aa  
 $q^2$  = frequency of genotype aa

Let us designate individuals of dominant phenotype by D, those of blending phenotype by I, and those of recessive phenotype by R. Table I shows all the possible types of matings, their frequencies, and also the relative frequencies of the six possible dizygotic twin or sib pair combinations.

Totaling, we find the frequencies of the various types of pairs to be as follows:

$$\begin{aligned}
 DD &= p^4 + p^3q + \frac{1}{4}p^2q^2 = \frac{1}{4}p^2(1 + p)^{2*} \\
 II &= p^3q + 3p^2q^2 + pq^3 = p(1 - p)(1 + p - p^2) \\
 RR &= \frac{1}{4}p^2q^2 + pq^3 + q^4 = \frac{1}{4}(1 - p)^2(2 - p)^2 \\
 DI &= 2p^3q + p^2q^2 = p^2(1 - p^2) \\
 RI &= 2pq^3 + p^2q^2 = p(1 - p)^2(2 - p) \\
 DR &= \frac{1}{2}p^2q^2 = \frac{1}{2}p^2(1 - p)^2
 \end{aligned}$$

In an allelomorph pair where dominance is complete, individuals would necessarily be D or R, and pairs DD, DR and

TABLE I

	MATINGS	OFFSPRING					
		DD	II	RR	DI	RI	DR
$p^4$	$\begin{matrix} \sigma \\ AA \end{matrix} \times \begin{matrix} \text{♀} \\ AA \end{matrix}$	$p^4$	0	0	0	0	0
$2p^3q$	$AA \times Aa$	$\frac{1}{2}p^3q$	$\frac{1}{2}p^3q$	0	$p^3q$	0	0
$p^2q^2$	$AA \times aa$	0	$p^2q^2$	0	0	0	0
$2p^3q$	$Aa \times AA$	$\frac{1}{2}p^3q$	$\frac{1}{2}p^3q$	0	$p^3q$	0	0
$4p^2q^2$	$Aa \times Aa$	$\frac{1}{4}p^2q^2$	$p^2q^2$	$\frac{1}{4}p^2q^2$	$p^2q^2$	$p^2q^2$	$\frac{1}{2}p^2q^2$
$2pq^3$	$Aa \times aa$	0	$\frac{1}{2}pq^3$	$\frac{1}{2}pq^3$	0	$pq^3$	0
$p^2q^2$	$aa \times AA$	0	$p^2q^2$	0	0	0	0
$2pq^3$	$aa \times Aa$	0	$\frac{1}{2}pq^3$	$\frac{1}{2}pq^3$	0	$pq^3$	0
$q^4$	$aa \times aa$	0	0	$q^4$	0	0	0

RR. The frequency of DD pairs would be the sum of the frequencies of DD, II, and DI pairs with incomplete dominance which equals  $\frac{1}{4}p(4 + 5p - 6p^2 + p^3)$ . Similarly, the frequency of DR pairs would equal the sum of DR and RI pairs with incomplete dominance, which is  $\frac{1}{2}(1 - p)^2(4 - p)$ . The frequency of RR pairs would be the same for complete as for incomplete dominance,  $\frac{1}{4}(1 - p)^2(2 - p)^2$ .

\*The writer is indebted to Mr. C. W. Cotterman for aid in the simplification of formulae.

TABLE IIA

GENE FREQUENCIES P Q		SINGLE PAIR FACTORS WITH BLENDING					
		DD	II	RR	DR	DI	RI
.01	.99	.0000255025	.00999801	.9703235025	.000049005	.00009999	.01950399
.05	.95	.00068906	.04975625	.857937065	.001128125	.00249375	.08799375
.10	.90	.003025	.0981	.731025	.00405	.0099	.1539
.15	.85	.0074328125	.14370625	.6182453125	.008128125	.02199375	.20049375
.20	.80	.0144	.1856	.5184	.0128	.0384	.2304
.25	.75	.0244140625	.22265625	.4306640625	.017578125	.05859375	.24609375
.30	.70	.038025	.2541	.354025	.02205	.0819	.2499
.35	.65	.0558140625	.27925625	.2875640625	.0258781255	.10749375	.24399375
.40	.60	.0784	.2976	.2304	.0288	.1344	.2304
.45	.55	.1064390625	.30875625	.1816890625	.030628125	.16149375	.21099375
.50	.50	.140625	.3125	.140625	.03125	.1875	.1875
.55	.45	.1816890625	.30875625	.1064390625	.030628125	.21099375	.16149375
.60	.40	.2304	.2976	.0784	.0288	.2304	.1344
.65	.35	.2875640625	.27925625	.0558140625	.0258781255	.24399375	.10749375
.70	.30	.354025	.2541	.038025	.02205	.2499	.0819
.75	.25	.4306640625	.22265625	.0244140625	.017578125	.24609375	.05859375
.80	.20	.5184	.1856	.0144	.0128	.2304	.0384
.85	.15	.6182453125	.14370625	.0074328125	.008128125	.20049375	.02199375
.90	.10	.731025	.0981	.003025	.00405	.1539	.0099
.95	.05	.857937065	.04975625	.00068906	.001128125	.08799375	.00249375
.99	.01	.9703235025	.00999801	.0000255025	.000049005	.01950399	.00009999

TABLE II<sub>B</sub>

GENE FREQUENCIES		COMPLETE DOMINANCE		
p	q	DD	DR	RR
.01	.99	.0101235025	.019552995	.9703235025
.05	.95	.05293906	.089121875	.857937065
.10	.90	.111025	.15795	.731025
.15	.85	.1731328125	.208621875	.6182453125
.20	.80	.2384	.2432	.5184
.25	.75	.3056640625	.263671875	.4306640625
.30	.70	.374025	.27195	.354025
.35	.65	.4425640625	.269871875	.2875640625
.40	.60	.5104	.2592	.2304
.45	.55	.5766890625	.241621875	.1816890625
.50	.50	.640625	.21875	.140625
.55	.45	.7014390625	.192121875	.1064390625
.60	.40	.7584	.1632	.0784
.65	.35	.8108140625	.133371875	.0558140625
.70	.30	.858025	.10395	.038025
.75	.25	.8994140625	.076171875	.0244140625
.80	.20	.9344	.0512	.0144
.85	.15	.9624453125	.030121875	.0074328125
.90	.10	.983025	.01395	.003025
.95	.05	.995687065	.003621875	.00068906
.99	.01	.9998255025	.000148995	.0000255025

Table II shows the expected ratios of the various types of pairs, for different values of p and q, for both complete and incomplete dominance. It can readily be seen that the amount of information concerning the inheritance of a trait conveyed by obtaining the ratios of the various types of pairs depends upon the number of pairs studied, and also, to some degree, upon the frequencies of the genes involved. If the frequency of the recessive gene (where dominance is complete) were .80, the ratio obtained from the various types of pairs is approximately the same as when q has a frequency of .60, but in this

instance the total numbers of the two phenotypes in the population studied would enable us to determine which gene was dominant. At a frequency of approximately .70 for  $q$ , DD and RR pairs occur with equal frequency, and DR pairs at their maximum frequency, .27+. We would not, of course, determine which phenotype was dominant. If, in a group of dizygotic twins or sib pairs, the percentage of DR pairs significantly exceeds 27%, variation in the trait cannot be due solely to inheritance, based on a single pair of autosomal genes with complete dominance.

TABLE III

Frequencies	Matings	$\sigma^{\circ} \sigma^{\circ}$			$\text{♀} \text{♀}$			$\sigma^{\circ} \text{♀}$		
		DD	DR	RR	DD	DR	RR	DD	DR	RR
$p^3$	$\sigma^{\circ} \text{A} \times \text{♀AA}$	$p^3$	0	0	$p^3$	0	0	$p^3$	0	0
$2p^2q$	$\text{A} \times \text{Aa}$	$\frac{1}{2}p^2q$	$p^2q$	$\frac{1}{2}p^2q$	$2p^2q$	0	0	$p^2q$	$p^2q$	0
$pq^2$	$\text{A} \times \text{aa}$	0	0	$pq^2$	$pq^2$	0	0	0	$pq^2$	0
$p^2q$	$\text{a} \times \text{AA}$	$p^2q$	0	0	$p^2q$	0	0	$p^2q$	0	0
$2pq^2$	$\text{a} \times \text{Aa}$	$\frac{1}{2}pq^2$	$pq^2$	$\frac{1}{2}pq^2$	$\frac{1}{2}pq^2$	$pq^2$	$\frac{1}{2}pq^2$	$\frac{1}{2}pq^2$	$pq^2$	$\frac{1}{2}pq^2$
$q^3$	$\text{a} \times \text{aa}$	0	0	$q^3$	0	0	$q^3$	0	0	$q^3$

In a trait where dominance is incomplete, the situation is more complex, because there are six instead of three types of pairs. Consequently, a much larger number of pairs would be necessary to obtain an accurate ratio. There is some compensation for this difficulty, in that where six instead of three types of pairs are included in the ratio, the precision of our ratios is likewise greater. If not enough pairs can be collected for significant ratios of all six types, pairs may be classed as concordant or discordant, the former group being the sum of DD, II and RR pairs, and the latter group the sum of DI, RI and DR pairs. Where dominance is complete, concordant pairs would of course include DD and RR pairs, and discordant would still include only DR.

There has been considerable data brought together by various investigators, giving ratios of concordant to discordant

dizygotic twin pairs, in respect to a number of traits. Unfortunately, almost without exception, only one type of concordant pair is considered, and moreover, the twins have been selected for the trait in question. Thus we have no way of knowing, from such data alone, the frequencies of the various phenotypes in the population as a whole.

#### SEX-LINKED FACTORS

When dealing with sex-linked factors, we have nine types of pairs, depending on sex as well as trait phenotype. Table III shows the various types of matings, and the ratios of the various types of pairs.

Totaling, we find the frequency of each type of combination to be as follows:

$$\begin{aligned}
 DD \ \sigma &= p^3 + \frac{1}{2} p^2 q + \frac{1}{2} p q^2 = \frac{1}{2} p (1 + p) \\
 DR \ \sigma &= p^2 q + p q^2 = p (1 - p) \\
 RR \ \sigma &= q^3 + \frac{1}{2} p q^2 + \frac{1}{2} p^2 q = \frac{1}{2} (1 - p) (2 - p) \\
 DD \ \text{♀} &= p^3 + 3 p^2 q + \frac{1}{2} p q^2 = \frac{1}{2} p (3 - p^2) \\
 DR \ \text{♀} &= p q^2 = p (1 - p)^2 \\
 RR \ \text{♀} &= q^3 + \frac{1}{2} p q^2 = \frac{1}{2} (1 - p)^2 (2 - p) \\
 DD \ \sigma \ \text{♀} &= p^3 + 2 p^2 q + \frac{1}{2} p q^2 = \frac{1}{2} p (1 + 2 p - p^2) \\
 DR \ \sigma \ \text{♀} &= p^2 q + 2 p q^2 = p (1 - p) (2 - p) \\
 RR \ \sigma \ \text{♀} &= \frac{1}{2} p q^2 + q^3 = \frac{1}{2} (1 - p)^2 (2 - p)
 \end{aligned}$$

Table IV shows the various ratios for the three types of pairs for various gene frequencies. It will be noted that the varying percentages of discordant male pairs form a symmetrical distribution, the highest value being .25 where both genes have a frequency of .50. This frequency is, of course, the same as that for random male pairs in the general population. While the fact that nine types of pairs existing in sex-linked factors introduces greater complications, there is some compensation in that differences in the occurrence in the two sexes would rather easily become apparent, and the only other type of inheritance likely to show such sexual discrepancies would be that involving sex-influenced factors.

#### SEX-INFLUENCED FACTORS

In a single factor trait which shows reversal of dominance in the two sexes, we can readily obtain the expected ratios at various gene frequencies for both male and female pairs by reference to Table II. Suppose, for example, male pairs fit

TABLE IV

P.	Q.	♂ ♀			SEX-LINKED FACTORS ♂ ♂			♀ ♀		
		DD	DR	RR	DD	DR	RR	DD	DR	RR
.01	.99	.0050995	.019701	.9751995	.00505	.0099	.98505	.0149995	.009801	.9751995
.05	.95	.0274375	.092625	.8799375	.02625	.0475	.92625	.07493755	.045125	.8799375
.10	.90	.0595	.171	.7695	.055	.09	.855	.1495	.081	.7695
.15	.85	.0958125	.235875	.6683125	.08625	.1275	.78625	.2233125	.108375	.6683125
.20	.80	.136	.288	.576	.12	.16	.72	.296	.128	.576
.25	.75	.1796875	.328125	.4921875	.15625	.1875	.65625	.3671875	.140625	.4921875
.30	.70	.2265	.357	.4165	.195	.21	.595	.4365	.1470	.4165
.35	.65	.2760625	.375375	.3485625	.23625	.2275	.53625	.5035625	.147875	.3485625
.40	.60	.328	.384	.288	.28	.24	.48	.568	.144	.288
.45	.55	.3819375	.383625	.2344375	.32625	.2475	.42625	.6294375	.136125	.2344375
.50	.50	.4375	.375	.1875	.375	.25	.375	.6875	.1250	.1875
.55	.45	.4943125	.358875	.1468125	.42625	.2475	.32625	.741825	.111375	.1468125
.60	.40	.552	.336	.112	.48	.24	.28	.792	.096	.112
.65	.35	.6101875	.307125	.0826875	.53625	.2275	.23625	.8376875	.079625	.0826875
.70	.30	.6685	.273	.585	.595	.21	.195	.8785	.063	.0585
.75	.25	.7265625	.234375	.0390625	.65625	.1875	.15625	.9140625	.046875	.0390625
.80	.20	.784	.192	.024	.72	.16	.12	.944	.032	.024
.85	.15	.8404375	.146625	.0129375	.78625	.1275	.08625	.9679375	.019125	.0129375
.90	.10	.8955	.099	.0055	.855	.09	.055	.9855	.009	.0055
.95	.05	.9488125	.049875	.0013125	.92625	.0475	.02625	.9963125	.0023750	.0013125
.99	.01	.9899505	.009999	.0000505	.98505	.0099	.00505	.9998505	.000099	.0000496

single factor inheritance with complete dominance, with p at a frequency of .10, and q at a frequency of .90. If sex-influenced, female pairs should fit the same mode of inheritance, but at a value of .90 for p. and .10 for q.

TABLE V

P	Q	SEX-INFLUENCED FACTORS, ♂ ♀ PAIRS		
		DD	DR	RR
.01	.99	.0194794975	.019849005	.9609714975
.05	.95	.1499296875	.033634375	.8164359375
.10	.90	.151975	.10305	.744975
.15	.85	.1969359375	.263128125	.5399359375
.20	.80	.2256	.3328	.4416
.25	.75	.2412109375	.392578125	.3662109375
.30	.70	.246975	.44205	.310975
.35	.65	.2460609375	.480878125	.2730609375
.40	.60	.2416	.5088	.2496
.45	.55	.2366859375	.525628125	.2376859375
.50	.50	.234375	.53125	.234375
.55	.45	.2376859375	.525628125	.2366859375
.60	.40	.2496	.5088	.2416
.65	.35	.2730609375	.480878125	.2460609375
.70	.30	.310975	.44205	.246975
.75	.25	.3662109375	.392578125	.2412109375
.80	.20	.4416	.3328	.2256
.85	.15	.5399359375	.263128125	.1969359375
.90	.10	.744975	.10305	.151975
.95	.05	.8164359375	.033634375	.1499296875
.99	.01	.9606714975	.019849005	.0194794975

In unlike-sexed pairs, we find upon examination of Table I, the following ratios:

$$\begin{aligned}
 DD &= 2p^3q + \frac{3}{4} p^2q^2 + p^4 = \frac{1}{4}p^2(3 - p(1 + p)) \\
 DR &= 2p^3q + 2pq^3 + 4.5p^2q^2 = p(1 - p)(4 + p - p^2) \\
 RR &= 2pq^3 + \frac{3}{4} p^2q^2 + q^4 = \frac{1}{4}(1 - p)^2(4 - p^2)
 \end{aligned}$$

Table V gives the ratios at various gene frequencies.

It can readily be seen that where a trait is dependent solely on heredity, based on a single pair of allelomorphs, the ratio of concordant pairs and discordant pairs may be of value in suggesting the mode of inheritance. Just how precise the information may be depends upon the number of pairs investigated, and the gene frequencies. If no discordant pairs are found in identical twins, and if fraternal twins show significantly more than 27% of discordant pairs, where only two phenotypes are known and where the sex of the pairs does not affect the ratios, we can be sure that more than a single pair of genes is involved in the expression of the trait in question.

TABLE VI

Matings	Frequency	Proportion of Discordant Pairs in Progeny	Proportion of Total
$\begin{matrix} \sigma \\ AO \end{matrix} \times \begin{matrix} \text{♀} \\ AA \end{matrix}$	.0245	0	0
AO × AO	.1225	.375	.0459375
AO × OO	.1575	.5	.07675
AO × BB	.00175	.5	.00875
AO × BO	.03325	.75	.0264375
AO × AB	.01050	.5	.00525
AA × AA	.0049	0	0
AA × AO	.0245	0	0
AA × OO	.0315	0	0
AA × BB	.00035	0	0
AA × BO	.00665	.5	.003375
AA × AB	.00210	.5	.00105
OO × AA	.0315	0	0
OO × AO	.1575	.5	.07875
OO × OO	.2025	0	0
OO × BB	.00225	0	0
OO × BO	.04275	.5	.021375
OO × AB	.0135	.5	.00675
BB × AA	.00035	0	0
BB × AO	.00175	.5	.00875
BB × OO	.00225	0	0

TABLE VI—[Continued]

Matings	Frequency	Proportion of Discordant Pairs in Progeny	Proportion of Total
$\begin{matrix} \text{♂} \\ \text{BB} \times \text{BB} \\ \text{♀} \end{matrix}$	.00025	0	0
BB × BO	.000475	.5	.0002375
BB × AB	.00015	.5	.000075
BO × AA	.00665	.5	.003375
BO × AO	.03325	.75	.0264375
BO × OO	.04275	.5	.0213750
BO × BB	.000475	0	0
BO × BO	.009025	.375	.00336975
BO × AB	.00285	.5	.001425
AB × AA	.00210	.5	.00105
AB × AO	.01050	.5	.00525
AB × OO	.0135	.5	.00675
AB × BB	.00015	.5	.000075
AB × BO	.00285	.5	.001475
AB × AB	.0009	.375	.0003375
		Total discordant	.35440725

## MULTIPLE ALLELOMORPHS

While it is possible to set up tables for ratios of various types of pairs at given gene frequencies for series of three or more allelomorphs, similar to those given for single pairs of allelomorphs, the complications are tremendously increased and their practical applications in determining modes of inheritance would not seem to be sufficient to justify their construction. If the frequencies of the various genes and their interactions are known, however, such knowledge may be of value in twin diagnosis. Let us consider how the blood groups may be of value in this connection.

Genes A and B show incomplete dominance in respect to each other, but both are dominant to gene O. The frequencies of these genes vary, of course, depending upon race. In North American Whites (Snyder, 1927) the relative percentages of the blood groups are approximately: A—42, O—45, B—10,

and AB—3. Allowing  $p$  to equal the frequency of gene A,  $q$  the frequency of gene B, and  $r$  that of O, we obtain the following genotypic ratio: AA—.07; AO—.35; BB—.005; BO—.095; OO—.45; and AB—.03. Let us now determine what percentage of fraternal twin and sib pairs would be expected to be discordant in blood group. As shown in Table VI, this can be accomplished by tabulating the frequency of all types of matings, and determining what percentage of paired offspring would be discordant. As shown in Table VI we should find such variation in approximately 35% of fraternal twins, in North American Whites.

Various research workers (Diehl and von Verschuer, 1933; Levit, 1935; Rife, 1934–37) have used blood grouping as confirmatory evidence of monozygosity, and in a total of several hundred pairs, assumedly monozygotic twins have never shown intra-pair variation in blood groups. There is the possibility, however, that selection for monozygosity may have been too rigid, and thus some less similar pairs of monozygotic twins classed as dizygotic. In a large group of twins, separated into classes according to zygoty, we should expect, if selection for monozygosity has not been too rigid, approximately 65% of the dizygotic twins to be of the same blood group. If the percentage of concordance exceeds this figure significantly, we may be justified in assuming that selection for identity has been too rigid, and that some of the assumedly dizygotic twins are monozygotic.

The M and N blood reactions may also be of use in this connection. In North American Whites (Wiener, 1934; Hyman, 1935) the relative proportions of the three types are MN—50, M—28, and N—22. M and N are a pair of allelomorphs lacking dominance. The frequency of gene M is therefore .53 and that of N, .47. Referring to Table IIa, we find that the ratio of discordant types (sum of ratios in columns 4, 5 and 6) in blending inheritance, with gene frequencies of from .45–.55 to .50–.50 is approximately 40%. As the M and N genes and the blood group genes have been shown not to be linked (Wiener, 1932), the proportion of sib and dizygotic twin pairs showing concordance in both traits should approximate  $.65 \times .60 = .39$ . In a similar manner, more independent traits whose mode of inheritance and gene frequencies are known could be added to the formula, thereby increasing its efficiency.

## CONCLUSIONS

Comparisons of identical with fraternal twins are of primary importance in obtaining partial evaluations of the relative roles played by heredity and environment in bringing about variation in human traits. Where simple types of inheritance are involved, data obtained from fraternal twins may be of value in suggesting the exact mode of inheritance. Such data, while not affording the most efficient method for determining manners of inheritance, are valuable by-products of twin studies primarily designed with other objectives in mind. In twin diagnosis, data taken from assumedly dizygotic twins concerning the occurrence of traits, whose manners of inheritance are known, may be of value in determining whether or not selection for monozygosity has been too rigid.

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