A search for assortative mating and segregation abnormalities among mother-child-father triplets from paternity cases

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A sample of more than 1000 triplets of mother-child-putative father from paternity cases rigorously tested for several genetic marker systems has been used to search for significant deviations from random mating and from expected segregation ratios. The criteria used to select families where the alleged man is with high probability the true father were found to induce biases in the material. Apart from these biases, there are few deviations from expected frequencies. A positive assortative mating is found for the P blood group system, and in the Gm immunoglobin system a maternal influence on the child's phenotype is indicated.

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The causes behind the globally occurring polymorphisms of blood groups and proteins in man are mainly unknown. We do not know if they are relics of diversifying environmental influences in man's early history which have not yet been equalized, or if they are still actively supported by selection.

One way to confirm the existence of selection is segregation analyses. To be informative these must comprise large numbers of families, and data usually have to be compiled from many sources.

Another aspect of human population structure concerns the mating system. Assortative mating is known to occur for many physical and mental traits, but it would be more surprising to find it for biochemical variants which are not readily known to the individual.

In this paper we report attempts to study assortative mating and segregation within mating groups for a number of blood and serum groups and allozyme proteins used as genetic markers.

Material and methods

The material used was obtained from the Swedish State Institute for blood group serology, and consists of 1036 triplets of mother-child-alleged father from paternity cases, mainly from the years 1971–1973. It has previously been used in an investigation on linkage disequilibrium by RASMUSON et al. (1979), in which the material is presented in detail.

It may seem inappropriate to use this type of families for segregation analyses, but the cases used were selected from a much larger material under criteria which should give a high probability that the alleged man was the true father. The criteria were as follows:

1) There was only one alleged man or all but one had been excluded;

2) the man was not excluded as father in tests where the theoretical exclusion probability exceeded 80%;

3) the paternity index value for the man in the primary, routinely performed test was higher than 19, and the total index value in an extended investigation exceeded 9.

The routinely performed tests during these years comprised 11 systems (see Table 1, left column) with a joint theoretical exclusion rate of about 86%. In most cases they were supplemented by tests for other systems (Table 1, right column), and the maximal theoretical exclusion rate was 93%.

The paternity index \( I \) compares the alleged man with a random man from the population as to the likelihood of being the father, when the phenotypes of mother and child are given:

\[ I = P_{\text{CMP}}/P_{\text{CM}} \]
Table I. Genetic marker systems used in paternity tests. The primary tests are routinely performed in all cases

| Primary tests          | Extended tests              |
|------------------------|-----------------------------|
| A.A2B0                 | P                            |
| MNSs                   | Kidd, Jk(a)                  |
| Rh                     |                             |
| Kell, K                |                             |
| Duffy, Fy(a)           |                             |
| haptoglobin, Hp-α      | serum complement, component, C3 |
| group-specific component, Gc | immunoglobulin, Inv |
| lipoprotein factor, Ag (x) | immunoglobulin, Gm(1,2) |
| acid phosphatase, AcP-I | adenosine deaminase, ADA*    |
| phosphoglucomutase, PGM-1 | glutamic pyruvic transaminase, GPT |
| adenylate kinase, AK   | 6-phosphogluconate dehydrogenase, 6-PGD |

* Included among the primary tests in 1972.

$I$ is then a ratio of two probabilities for the child's phenotype, one if the man is the true father, the other if the father is a random man from the population. The value of $I$ is computed for each genetic system from the phenotypes of the triplet and the gene frequencies in the population. The overall value is obtained by multiplication of the separate values. A value of $I = 19$ corresponds to a relative probability of 95% for the man being the true father, thus the conventional border of significance. $I = 9$ means a probability of 90%.

The above criteria, taken together, will give a high probability that the alleged men are the true fathers, and thus allow the use of the families in studies of assortative mating and segregation analyses. However, the demand of high index values was found to give rise to some peculiar distributions of mating types and segregating offspring, which reduced the information that could be obtained from the material. These will be discussed in relation to the results.

The complex systems, MNSs, Rh and Gm have been separated on subsystems, viz. MN and S, RhC, RhD, and RhE, Gm(1) and Gm(2), giving a total of 23 systems. Of these, ten show dominance, ten are codominant and three are multiallelic.

For each codominant and multiallelic system the material has been tested for goodness of fit to mating frequencies expected from equal gene frequencies for males and females, phenotypic frequencies in accordance to Hardy-Weinberg equilibrium, and random mating. Males and females have also been tested for homogeneity of phenotypic distributions (or gene frequencies for codominant systems) and separately for accordance to Hardy-Weinberg equilibrium.

The effect of pooling reciprocal matings has been investigated, and, where possible, also the pooling of all matings into only four types, according to homozygosity or heterozygosity of the parents.

When the assumptions of Hardy-Weinberg equilibrium and equal gene frequencies for mothers and fathers are relaxed, a simple test of homogeneity will show if the distribution on different mating types deviates from randomness. Such tests have also been performed, including all phenotypic classes, as well as after pooling to homozygotes and heterozygotes. In order to avoid a possible influence of small expected numbers, rare mating classes have been pooled in some systems. Further, $A_1$ and $A_2$ in the ABO system as well as RhC and RhCw have been pooled. Results of tests both with and without pooling are given.

In systems with dominance, only two phenotypes, $D$ (= dominant) and $R$ (= recessive) can be discerned, and four mating combinations $D \times D$, $D \times R$, $R \times D$, $R \times R$. Goodness of fit relates to equal distribution in males and females, and random combination. The occurrence of deviations between reciprocal matings has also been tested. When pooling the reciprocals, a result is obtained which is equal to a $2 \times 2$ contingency test.

In the segregation analyses, the offspring from each mating combination with segregation possibilities has been tested against expected numbers, if the total offspring exceeded five (or 14
if more than two classes were expected). For systems with dominance, the expected numbers were computed from gene frequencies estimated in the parental population. Since the material consists of only one-child families no correction for different family size is needed.

Results

Mating types

In Table 2A, the $\chi^2$ values for observed deviations and their significances in the various tests are given for the systems included in the primary tests. There are seven codominant or multiallelic systems with highly significant deviations in goodness of fit (tests I, II and III): ABO, RhC, AcP, MN, PGM, Hp and Gc. In all these except the ABO system the deviations were caused by a pronounced excess of homozygotes among males, and can be explained as a bias of the sampling procedure, since homozygous males generally have higher index values than heterozygotes. This bias has consequences for all goodness of fit tests but not for homogeneity.

In the ABO system, males and females taken separately are in Hardy-Weinberg equilibrium, but the frequencies of B and 0 types show heterogeneity between sexes, which gives significant deviations from expected mating type frequencies (test I and II) and also from equality of reciprocals (I-1). A tendency to negative assortative mating, especially between A and non-A, causes heterogeneity (test IV). All these deviations can be ascribed to the sampling bias, since low index values are obtained when both parents are of type A, and fathers which are B or AB give especially high index values when the mother is 0 and the child inherits the B gene. The pooling of A and A2 does not cause any conclusive changes in the results.

The significant heterogeneity in test V for the MN system indicates assortative mating, since it is not due to heterogeneity between males and females. It turns out to be three combinations which are in excess, viz. N x M, MN x MN and M x M (Table 3A), whereas there is a deficit of combinations N x MN and MN x M. These deviations cannot be wholly explained by the index values.

Among the dominant systems in Table 2A, there is one, RhD, where reciprocal mating types have different frequencies (I–II is significant). As shown in Table 3B, there is an excess of $D^+ Q \times D^- \sigma$ over the reciprocal mating type. In accordance to this there is heterogeneity between sexes, but no indication of assortative mating (test IV).

In the remaining systems among those applied in the primary paternity tests the goodness of fit is acceptable. These include two codominant systems, RhE and AK, and four with dominance, S, K, Fy(a) and Ag(x).

Among the systems used in extended paternity tests (Table 2B), there are significant deviations in only one codominant system, ADA, and two systems with dominance, Jk(a) and P. The ADA system shows a deficit of matings 1–2 mother with 1–1 father (Table 3C), which gives the significant deviation in test III of Table 2B. This deficit also results in a heterogeneity of gene frequencies between males and females, and significance in test IV. There is no obvious explanation for this, except that the underrepresented combination gives rather low index values.

The Jk(a) system shows the same type of deviation as RhD, only with higher significance. There is an excess of mating a– $Q \times a^+ \sigma$ (Table 3D), heterogeneity between sexes, but not assortative mating.

In the P system, goodness of fit as well as homogeneity are unsatisfactory, but not due to heterogeneity between sexes. Instead, there is an excess of matings between equals, $P^+ \times P^+$ and $P^- \times P^-$ (Table 3E), thus a case of positive assortative mating.

Segregation analyses

Each mating combination has been studied separately for the segregation of the offspring. Table 4A–C shows the results as to which class is in excess and the significance of the deviations. Because of its low frequency, combinations with RhCw all have offspring numbers below 10. Therefore no distinction has been made between C and Cw, and the RhC system has been included among the systems with two codominant alleles (Table 4B).

Also for the segregation, the impact of index values may bias the results. All segregation classes have been related to the index value of that special mother-father-child combination in order to judge its importance in this material. Most cases of significant deviations from expectations show an excess of the offspring class with the highest index value, but there are a few exceptions as shown by the italicizations in Table 4. The 6-PGD
Table 2A and B. Evaluation of deviations found in tests for goodness of fit and homogeneity. Goodness of fit is to Hardy-Weinberg expectations for males and females separately, and to mating type frequencies expected with equal gene frequencies and random mating (test I, II, III). The tested homogeneity of males vs. females concerns phenotype frequencies, or gene frequencies in codominant systems. Mating type frequencies without the condition of equal phenotype distributions in males and females are examined in homogeneity tests (IV and V).

N = number of matings; df = degrees of freedom

Test I and IV: all phenotypic classes separated
Test II: reciprocal mating combinations pooled
Test III and V; phenotypes pooled into two classes, homozygotes and heterozygotes

* Effect of pooling reciprocals in III
* P < 0.05; ** P < 0.01; *** P < 0.001

A. Primary tests

| Test systems | N    | Goodness of fit | I       | II      | III     | I-II    | Homogeneity | IV    | V    |
|--------------|------|----------------|---------|---------|---------|---------|-------------|-------|------|
|              |      |                | \(\chi^2\) | df \(\chi^2\) | df \(\chi^2\) | df \(\chi^2\) | df \(\chi^2\) vs. 2 df | \(\chi^2\) | df \(\chi^2\) |
| multiallelic |      |                |         |         |         |         |             |       |      |
| A, B         | 1036 | 1.2            | 1.8     | 61.5*** | 32      | 30.5*   | 17         | 31.0**  | 15  | A<0.09    | 47.4**  | 25  |
| AB0          |      | 0.8            | 46.9*** | 13      | 21.9**  | 7        | 25.0**     | 6     | A<0.4     | 31.8**  | 9   |
| RHCW         | 1036 | 19.7***        | 3.8     | 38.5*   | 22      | 28.1**  | 12         | 10.4    | 10 | c<0.2     | 12.4    | 16  |
| RHC          |      | 14.1***        | 2.6     | 19.3**  | 7       | 14.9**  | 4          | 15.8*** | 2  | 4.4       | 3.1     | 4   |
| AcP          | 1029 | 8.7**          | 0.8     | 42.4**  | 22      | 31.1*** | 12         | 11.3    | 10 | A:1.7     | 13.1    | 16  |
| codominant   |      |                |         |         |         |         |             |       |      |
| MN           | 1034 | 16.7***        | 5.6*    | 34.2*** | 7       | 28.4**  | 4          | 28.2*** | 2  | 5.8       | 3.1     | 4   |
| RhE          | 1036 | 7.0**          | 0.03    | 7.3     | 6       | 7.2     | 4          | 2.3     | 2  | 0.2       | 0.4     | 1   |
| PGM          | 1026 | 21.7***        | 1.49    | 37.4*** | 7       | 26.5**  | 4          | 14.2*** | 2  | 10.9*     | 3.0     | 6.9 |
| Hp           | 1011 | 23.7***        | 4.2*    | 41.3*** | 7       | 30.3**  | 4          | 26.6*** | 2  | 11.0*     | 3.6     | 5.3 |
| Gc           | 1031 | 29.2***        | 1.30    | 37.4*** | 7       | 25.8*** | 4          | 21.2*** | 3  | 11.6**    | 3.1     | 2.5 |
| AK           | 1022 | 0.5            | 0.3     | 4.0     | 7       | 2.8     | 4          | 2.4     | 2  | 1.2       | 3.0     | 3.6 |
| with dominance |    |                |         |         |         |         |             |       |      |
| S            | 954  | 2.6            | 2       | 1.8     | 1       | 0.8     | 1          | 0.8     | 1  | 1.8       | 1       | 1   |
| RhD          | 1033 | 4.4            | 2       | 0.02    | 1       | 4.4*    | 1          | 4.1*    | 1  | 0.007     | 1       | 1   |
| K            | 1023 | 0.6            | 2       | 0.007   | 1       | 0.6     | 1          | 0.4     | 1  | 0.008     | 1       | 1   |
| Fy(a)        | 969  | 0.4            | 2       | 0.1     | 1       | 0.3     | 1          | 0.3     | 1  | 0.1       | 1       | 1   |
| Ag(a)        | 1029 | 2.6            | 2       | 0.1     | 1       | 2.4     | 1          | 2.3     | 1  | 0.1       | 1       | 1   |

B. Extended tests

| Test systems | N    | Goodness of fit | I       | II      | III     | I-II    | Homogeneity | IV    | V    |
|--------------|------|----------------|---------|---------|---------|---------|-------------|-------|------|
|              |      |                | \(\chi^2\) | df \(\chi^2\) | df \(\chi^2\) | df \(\chi^2\) | df \(\chi^2\) vs. 2 df | \(\chi^2\) | df \(\chi^2\) |
| codominant   |      |                |         |         |         |         |             |       |      |
| C3           | 306  | 1.0            | 0.4     | 5.6     | 7       | 2.6     | 4          | 2.1     | 2  | 3.0       | 3.7     | 3.9 |
| ADA          | 740  | 0.001          | 0.5     | 7.4     | 4       | 2.6     | 2          | 6.9*    | 2  | 4.6*      | 1*     | 4.9*|
| GPT          | 84   | 0.2            | 0.1     | 4.8     | 7       | 3.8     | 4          | 0.6     | 2  | 1.0       | 3.1     | 4.5 |
| 6-PGD        | 392  | 0.2            | 0.3     | 0.5     | 2       | 0.05    | 1          | 0.5     | 2  | 0.4       | 0.3     | 0.04|
| with dominance |    |                |         |         |         |         |             |       |      |
| P            | 546  | 9.9**          | 2       | 9.9**   | 2       | 9.9**   | 1          | 0.07    | 1  | 0.2       | 9.9**   | 1   |
| Jk(a)        | 381  | 25.3***        | 2       | 2.1     | 1       | 23.1*** | 1          | 22.3*** | 1  | 0.8       | 1       | 1   |
| Inv          | 132  | 2.8            | 2       | 0.0004  | 1       | 2.9     | 1          | 2.4     | 1  | 0.06      | 1       | 1   |
| Gm(1)        | 312  | 0.2            | 0.0006  | 1       | 0.2     | 0.2     | 1          | 0.2     | 1  | 0.001     | 1       | 1   |
| Gm(2)        | 257  | 1.9            | 2       | 1.5     | 1       | 0.5     | 1          | 0.4     | 1  | 1.1       | 1       | 1   |
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Table 3A–E. Mating type frequencies in systems with significant deviations from expectation, not possible to explain from bias in selecting families with high paternity index. In mating combinations the type of the mother is given first.

In expected with equal gene frequencies in males and females, random mating, and HW equilibrium (the last only for codominant systems).

IV: expected from random mating.

system has a significant surplus of 1–2 offspring from the parental combination 1–2 × 1–1, which is contrary to expectation from index values. However, the total number is only 18 and the difference in index value is small (1.126 against 1.0), so the importance of this discrepancy is dubious.

A second case of discrepancy between index value and excess class is found in the Gm(2) system, where two mating types have significant deviations contrary to the relative index values. Also the Gm(1) and the joint Gm(1, 2) system reveal the same tendency, which most probably can be attributed to a maternal influence. It is known that there is a passive transfer of IgG from the mother via the placenta, and the phenotype of the child during the first year need not correspond to its genotype (HARBOE and LUNDEVALL 1961). This is also true for the Inv system, where the same type of deviations from expectations are found, although not significant.

All other significant discrepancies from expected frequencies are in accordance with the selection of families with high index values, and can therefore not be taken as criteria of abnormal segregation.

Discussion

The selection of families with high paternity index causes very special biases for most of the systems, especially those included in the primary testing. It is not clear why the RhE and AK systems alone of the codominant primary systems do not show the excess of homozygotes found in the other systems. As to RhE, the index value that was used had been calculated from the compound Rh system where variation in the E subunit might have less impact. In the AK system, one of the alleles has a very low frequency. A comparison to the ADA system with about equal gene frequencies, however, reveals opposite kinds of bias. AK shows an acceptable goodness of fit for mating frequencies, but there is a highly significant departure from expected segregation in the offspring. For the ADA system the situation is reversed, with no segregation abnormalities but a significant bias in mating frequencies.
Table 4A-C. Segregation analysis. In mating combinations the type of the mother is given first. Classes in excess which are contrary to expectations from the relative index values are in italics.

N: number of families  = number of offspring

*: difference between observed and expected numbers < 1

** P < 0.05; *** P < 0.01; **** P < 0.001

* Designation of matings is inadequate for the MN, RhC and RhE systems; M, c and e correspond to 1; N, C+C*, and E to 2

A. Multiallelic systems

| Mating | N | Class in excess | goodness of fit | Mating | N | Class in excess | goodness of fit |
|--------|---|----------------|----------------|--------|---|----------------|----------------|
| A x A | 139 | A | 30.6*** | 2 | 119 | = | 0.008 | 1 |
| A 0 | 125 | 0 | 6.4* | 2 | 131 | BB | 1.3 | 1 |
| 0 x A | 57 | A | 16.9*** | 1 | 26 | CB | 9.8** | 1 |
| A x A | 36 | = | 0.008 | 1 | 19 | = | 0.05 | 1 |
| 0 x B | 40 | B | 3.1 | 1 | 31 | CB | 3.9* | 1 |
| B x A | 32 | 0 | 0.6 | 1 | 28 | CB | 1.7 | 1 |
| A x A | 91 | A | 0.7 | 2 | 155 | BA | 1.5 | 2 |
| A x A | 40 | A | 4.1 | 2 | 22 | CA | 5.3 | 3 |
| A x A | 42 | A | 6.7* | 2 | 15 | CA | 7.1 | 3 |
| A x B | 65 | A; B | 22.8*** | 5 | 73 | AA | 0.2 | 1 |
| B x A | 35 | A; B; A | 7.2 | 5 | 61 | AA | 0.4 | 1 |
| A x B | 10 | B | 1.6 | 1 | 44 | CA, CB | 4.0 | 1 |
| 0 x A | 28 | B | 2.3 | 1 | 33 | BB, BA | 3.1 | 3 |
| A x A | 6 | B | 2.7 | 1 | 10 | = | 0 | 1 |
| 0 x A | 8 | A | 0.5 | 1 | 9 | CA | 5.4* | 1 |
| B x A | 16 | = | 0.07 | 1 | 6 | = | 0.4 | 1 |
| A x A | 10 | = | 0.02 | 1 | 5 | = | 0.09 | 1 |
| B x A | 22 | B | 4.1 | 3 | 3 |
| B x A | 15 | A | 2.7 | 3 | 1 |

B. Codominant systems

| Mating* | N | Class in excess | x² (1) | Mating* | N | Class in excess | x² (1) | Mating* | N | Class in excess | x² (1) | Mating* | N | Class in excess | x² (1) |
|---------|---|----------------|-------|---------|---|----------------|-------|---------|---|----------------|-------|---------|---|----------------|-------|
| 1-1 x 1-2 | 152 | MN | 0.5 | 142 | M | 2.5 | 219 | N | 0.6 | 107 | N | 0.2 | 75 | N | 0.05 |
| 1-2 x 1-1 | 147 | RhC, C* | 0.2 | 179 | cc | 0.3 | 213 | cc | 2.9 | 91 | CC | 0.3 | 86 | CC | 2.3 |
| 1-2 x 1-2 | 198 | RhE | 7.3** | 205 | ee | 0.6 | 77 | Ee | 0.7 | 12 | EE | 0.3 | 8 | Ee | 0.5 |
| 1-2 x 2-2 | 188 | PGM | 17.9*** | 202 | 1-1 | 3.9* | 118 | 2-2 | 5.0 | 20 | 2-2 | 3.2 | 16 | 2-2 | 6.3* |
| 2-2 x 1-2 | 55 | Hp | 0.02 | 68 | 1-1 | 11.5*** | 181 | 1-1, 1-2 | 6.0* | 185 | 2-2 | 6.6* | 164 | 1-2 | 6.2* |
| 1-2 x 2-2 | 128 | Gc | 12.7*** | 205 | 1-1 | 0.6 | 130 | 2-2 | 5.5 | 38 | 2-2 | 1.7 | 24 | 2-2 | 4.2* |
| 1-2 x 1-2 | 82 | AK | 17.6*** | 78 | 1-1 | 1.8 | 3 | = | 0 | 0 | = | 0 | 0 | = | 0 |
| 1-2 x 1-2 | 3 | C1B | 3 | 2 | = | 3 | C1B | 3 | 2 | = | 3 | 2-2 | 2.3 | 54 | 2-2 | 0.07 |
| 1-2 x 1-2 | 85 | ADA | 0.6 | 57 | 1-1 | 0.2 | 14 | 2-2 | 3.1 | 0 | = | 0 | = | 0 | = |
| 1-2 x 1-2 | 13 | GPT | 1.9 | 7 | 1-2 | 3.6 | 21 | 1-2 | 1.3 | 10 | 2-2 | 1.6 | 9 | 1-2 | 1.0 |
| 1-1 x 1-1 | 14 | 6-PGD | 0.3 | 18 | 1-2 | 5.6* | 1 | = | 0 | = | 0 | = | 0 | = |
C. Systems with dominance

| Mating       | Class in excess | N  | Class in excess | N  | Class in excess | N  | Class in excess | \( \chi^2 \) |
|--------------|----------------|----|----------------|----|----------------|----|----------------|------------|
| \(- x + \)   |                |    |                |    |                |    |                |            |
| S            | 237 S*         | 7.1**| 215 S-         | 6.8**| 287 S*         | 1.2 |                |            |
| RhD          | 132 D*         | 0.9 | 166 D-         | 3.5 | 696 D*         | 0.8 |                |            |
| K            | 94 K*          | 22.2***| 83 =          | 0.01| 7 K*          | 2.2 |                |            |
| Fy(a)        | 219 a+         | 11.6***| 226 a-        | 3.2 | 406 a+        | 10.0**|                |            |
| Ag(x)        | 254 x*         | 11.1***| 220 x-        | 0.8 | 144 x*        | 0.8 |                |            |
| P            | 85 P*          | 0.2 | 95 P-          | 2.7 | 306 P*        | 6.8**|                |            |
| Jk(a)        | 113 a+         | 1.4 | 54 a-         | 0.8 | 181 =         | 0.02 |                |            |
| Inv          | 22 Inv-        | 0.4 | 12 =         | 0.2 | 3 =          |          |                |            |
| Gm(1)        | 71 I-          | 0.2 | 76 I+         | 2.8 | 121 I+        | 2.1 |                |            |
| Gm(2)        | 52 2-          | 7.8**| 49 2+         | 11.0***| 16 =        | 0.06 |                |            |

Apart from the bias due to the selection of the material, there are few deviations from expected frequencies in mating combinations or segregating offspring. Most interesting is the implied positive assortative mating in the P system. One possible explanation for this may be a regional heterogeneity of the material. If the P- phenotype is more common in one part of the country and the majority of mating are endogamous, this will give an excess of matings between equals. A regional heterogeneity has been demonstrated in Sweden (Beckman 1959), and in the present material there is also a significant heterogeneity between Scandinavians and non-Scandinavians, with frequencies of P- 0.5 and 0.62 respectively (Rasmuson et al. 1979). This heterogeneity alone is not enough to explain the observed mating distribution, even if all mating were within these two groups, which they are not. Regional heterogeneity is known to occur in Sweden also for several others of the genetic markers, and gene frequency differences between Scandinavians and non-Scandinavians were found, besides for the P system, also for K, Ag, PGM and some alleles in the AB0, AcP and Rh systems. No indications of a positive assortative mating was found in any of these systems. It is, however, clear that the assortative mating in the P system has to be confirmed in other materials before a biological explanation is called for.

Finally, the segregation deviations found in the Gm system indicate that the reliability of the system, when young children are concerned, may be questioned, since there is an excess of children with phenotype equal to that of the mother, especially for Gm(2).

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