

Thus, the elements responsible for variation in recombination frequencies segregate like genes and are indeed separable from the regions whose recombination they affect. We conclude that the elements are genes or gene systems.

4. SUMMARY

1. Frequencies of recombination between the component loci of the *A* and *B* incompatibility factors were determined for two monokaryotic strains and seven of their progeny after crossing to a common tester strain.

2. The tendencies for high and low recombination within each incompatibility factor are separable from the factors 'uemselves and segregate like genes.

3. The elements controlling recombination within the *A* and *B* factors segregate independently.

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5. REFERENCES

- KOLTIN, Y., RAPER, J. R., AND SIMCHEN, G. 1967. The genetic structure of the incompatibility factors of *Schizophyllum commune*: the *B* factor. *Proc. Natl. Acad. Sci., U.S.*, 57, 55-62.
- RAPER, J. R., BAXTER, M. G., AND ELLINGBOE, A. H. 1960. The genetic structure of the incompatibility factors of *Schizophyllum commune*: the *A*-factor. *Proc. Natl. Acad. Sci., U.S.*, 46, 833-42.
- SIMCHEN, G. 1967. Genetic control of recombination and the incompatibility system in *Schizophyllum commune*. *Genet. Res., Camb.*, 9, 195-210.
- STAMBERG, J. 1968. Two independent gene systems controlling recombination in *Schizophyllum commune*. *Molec. Gen. Genetics*, 102, 221-8.

AN EXCESS OF L^ML^N HETEROZYGOTES IN A SOUTH EUROPEAN POPULATION

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COMPARING theoretical and observed MN blood groups frequencies among the offspring of various parental combinations, Wiener (1943) noted that there was a significant excess of MN children in the mating MN × MN. He concluded that it was probably due to illegitimacies or errors in technique. Wiener gave the same explanation for the excess of L^ML^N heterozygotes which was found by Lattes and Garrasi (1932) in a sample of Italian population. It seems unlikely that such an explanation is correct for every case of overabundance of L^ML^N heterozygotes.

The present investigation is based on the records of the medico-legal analyses concerning 616 cases of disputed paternity examined by the courts

of Bosnia and Hercegovina (Yugoslavia) during the period between the years 1962 and 1967. There is no reason to doubt that a definite group of cases of disputed paternity represents a good random sample of a population, in respect of at least some of the individual characters which are involved in the medico-legal analyses.

TABLE 1
Frequency of the MN blood groups in the sample

| Parental combination | | Offspring | | | Total |
|----------------------|-----------------|-----------|-----|----|-------|
| Mother | Putative father | M | MN | N | |
| M | M | 36 | — | — | 36 |
| M | N | — | 17 | — | 17 |
| M | MN | 32 | 29 | — | 61 |
| N | M | — | 28 | — | 28 |
| N | N | — | — | 15 | 15 |
| N | MN | — | 32 | 20 | 52 |
| MN | M | 29 | 48 | — | 77 |
| MN | N | — | 38 | 16 | 54 |
| MN | MN | 31 | 214 | 31 | 276 |
| Total | | 128 | 406 | 82 | 616 |

1. THE FREQUENCY OF THE GENOTYPES

Table 1 shows the basic data about the frequency of the MN blood group in the sample examined.

The frequency of phenotypes in the two main subgroups of the sample (mothers+putative fathers and children) is summarised in table 2.

TABLE 2
Frequency of phenotypes in the subgroups of the sample

| | Frequency of phenotypes | | | Total |
|------------------------------|-------------------------|-----|-----|-------|
| | M | MN | N | |
| Mothers and putative fathers | 255 | 796 | 181 | 1232 |
| Children | 128 | 406 | 82 | 616 |

The percentage frequencies of the genotypes in the subgroups of the sample are given in table 3, together with the respective maximum likelihood estimates of the proportions of the allelomorphs (Wiener, 1935).

It may be pointed out that no significant difference exists between the parent and offspring subgroups of the sample regarding the frequencies of the genotypes and the allelomorphs. This observation could be interpreted as the evidence of constancy of the genetical make-up of the population, which is obviously true for the two consecutive generations under examination.

On the other hand, the frequencies of the genotypes observed in both sub-groups differ significantly from the corresponding values expected in an equilibrium population: a substantial excess of $L^M L^N$ heterozygotes is evident. Such a prominent excess of heterozygotes has not been reported

for any population previously studied, excepting several comparatively small samples of the Spanish population (Hors, 1951; Hors and Sarandeses, 1951; Hors and Marcos, 1951).

TABLE 3
Percentage frequency of the genotypes and the proportion of the genes in the subgroups of the sample

| | Percentage frequency of the genotypes | | | Proportion of the genes | |
|------------------------------|---------------------------------------|-------|-------|-------------------------|--------|
| | LMLM | LMLN | LNLN | LM | LN |
| Mothers and putative fathers | 20.70 | 64.61 | 14.69 | 0.5300 | 0.4700 |
| Children | 20.78 | 65.91 | 13.31 | 0.5373 | 0.4627 |

2. THE FREQUENCY OF MATING TYPES

It is reasonably justifiable to assume that the mother-putative father combinations have about the same value as the wife-husband pairs in indicating the properties of the mating system in the population. In table 4 the percentage frequencies of the mother-putative father combinations are given together with the corresponding expected frequencies of the phenotypes among their offspring. Theoretical percentage frequencies of the types of mating have been computed using the proportions of genotypes in the mothers + putative fathers subgroup of the sample (Percentage frequency of the genotypes, table 3), assuming that genotypes (phenotypes) mate at random.

TABLE 4
Percentage frequencies of the mating types and the expected percentage frequencies of the phenotypes in the offspring

| Type of mating | | Percentage frequency | | Theoretical percentage frequency of phenotypes in the offspring | | |
|----------------|-----------------|----------------------|----------|---|--------|--------|
| Mother | Putative father | Observed | Expected | M | MN | N |
| M | M | 5.84 | 4.24 | 5.84 | — | — |
| M | N | 2.76 | 3.04 | — | 2.76 | — |
| M | MN | 9.90 | 13.37 | 4.95 | 4.95 | — |
| N | M | 4.55 | 3.04 | — | 4.55 | — |
| N | N | 2.44 | 2.16 | — | — | 2.44 |
| N | MN | 8.44 | 9.49 | — | 4.22 | 4.22 |
| MN | M | 12.50 | 13.37 | 6.25 | 6.25 | — |
| MN | N | 8.77 | 9.49 | — | 4.385 | 4.385 |
| MN | MN | 44.80 | 41.75 | 11.20 | 22.40 | 11.20 |
| Total | | 100.00 | 100.00 | 28.240 | 49.515 | 22.245 |

A χ^2 test of the two distributions (the observed and the expected percentage frequencies of the types of mating) shows that they are not discrepant; this suggests that the phenotypes (genotypes) mate at random in respect of this gene difference.

3. THE EXPECTED FREQUENCY OF GENOTYPES IN THE OFFSPRING

It is quite clear that the genotypic proportions in the parental subgroup of the sample are not the equilibrium ones. According to the established fact of randomness of mating and to the rule that the equilibrium genotypic proportions should be reached after a single generation of random intermarriage (Wiener, 1931), one would expect to find substantial differences between the parental and offspring samples in respect of their phenotypic (genotypic) composition, but it is not so: the frequency of the genotypes (phenotypes) is nearly the same in both subgroups, as was shown earlier (table 3).

Table 5 shows the observed and the theoretically expected percentage frequencies of the phenotypes in the subgroup "Children" of the sample. It is clear that the two distributions are significantly discrepant.

TABLE 5

The observed and the expected percentage frequencies of the phenotypes in the offspring

| Distribution | Percentage frequency of phenotypes in the subgroup "children" | | |
|--------------|---|--------|--------|
| | M | MN | N |
| Observed | 20.78 | 65.91 | 13.31 |
| Expected | 28.240 | 49.515 | 22.245 |

The observed excess of $L^M L^N$ heterozygotes, which is quantitatively constant from one generation to the next, seems to be originating perpetually through the generations despite the randomness of mating. The available data make it possible to attempt an explanation of this unusual phenomenon.

4. THE FREQUENCY OF THE MOTHER-CHILD PAIRS

The theoretical percentage frequency of the mother-child combinations, given in table 6, can be easily derived from the data shown in table 4 (Theoretical percentage frequency of phenotypes in the offspring).

TABLE 6

Theoretical percentage frequencies of the mother-child combinations

| Mothers of type | Children of type (theoretical percentages) | | | Total |
|-----------------|--|--------|--------|---------|
| | M | MN | N | |
| M | 10.790 | 7.710 | — | 18.500 |
| MN | 17.450 | 33.035 | 15.585 | 66.070 |
| N | — | 8.770 | 6.660 | 15.430 |
| Total | 28.240 | 49.515 | 22.245 | 100.000 |

The expected percentages of different phenotypes in the offspring of each type of mothers are given in table 7.

TABLE 7

The expected percentage frequencies of the phenotypes in the offspring of each type of mothers

| Mothers of type | Children of type (expected percentage frequency) | | | Total |
|-----------------|---|-------|-------|--------|
| | M | MN | N | |
| M | 58.32 | 41.68 | — | 100.00 |
| MN | 26.41 | 50.00 | 23.59 | 100.00 |
| N | — | 56.84 | 43.16 | 100.00 |

The observed frequency and percentage frequency of the mother-child combinations in the sample are shown in table 8.

TABLE 8

The observed frequencies of the mother-child combinations in the sample

| Mothers of type | Children of type (observed frequency and percentages) | | | | | | Total | |
|-----------------|--|-------|-----|-------|----|-------|-------|--------|
| | M | | MN | | N | | | |
| | f | % | f | % | f | % | f | % |
| M | 68 | 11.04 | 46 | 7.47 | — | — | 114 | 18.51 |
| MN | 60 | 9.74 | 300 | 48.70 | 47 | 7.63 | 407 | 66.07 |
| N | — | — | 60 | 9.74 | 35 | 5.68 | 95 | 15.42 |
| Total | 128 | 20.78 | 406 | 65.91 | 82 | 13.31 | 616 | 100.00 |

The observed percentage frequency of the phenotypes in the offspring of each type of mothers is shown in table 9.

TABLE 9

The observed percentage frequency of the phenotypes in the offspring of each type of mothers

| Mothers of type | Children of type (observed percentage frequency) | | | Total |
|-----------------|---|-------|-------|--------|
| | M | MN | N | |
| M | 59.65 | 40.35 | — | 100.00 |
| MN | 14.74 | 73.71 | 11.55 | 100.00 |
| N | — | 63.16 | 36.84 | 100.00 |

χ^2 tests of the observed and expected distributions of the percentage distributions of the phenotypes in the offspring of each type of mothers (tables 7 and 9) give the results shown in table 10.

It may be noted that only the observed distribution of phenotypes in the offspring of MN mothers differs significantly from the theoretical expectation. This observation shows that the excess of $L^M L^N$ heterozygotes originates entirely from the mothers of the same genotype. In other words, the heterozygous mothers have a tendency to conceive and consequently to deliver more heterozygous children than is expected theoretically.

TABLE 10

Results of the χ^2 tests

| Mothers of type | Discrepancy between the observed and the expected distributions of phenotypes in the offspring | | |
|--------------------|--|---------|-------------|
| | χ^2 | P | Discrepancy |
| M | 0.073 | > 0.70 | No |
| MN | 22.545 | < 0.001 | Significant |
| N | 1.628 | > 0.10 | No |

5. SUMMARY

1. A sample of the population of Bosnia and Hercegovina (Yugoslavia) consisting of 616 cases of disputed paternity is examined.
2. An excess of $L^M L^N$ heterozygotes is found to exist.
3. The evidence is presented that the excess of heterozygotes is due to the excess of homospecific deliveries among MN mothers.

6. REFERENCES

- HORS, P. 1951. Séro-anthropologie du Léon. *4th Int. Congr. Blood Transfusion, Lisbon*, 352-353.
- HORS, P., AND MARCOS, G. 1951. Séro-anthropologie des "vaqueiros" en Asturie. *4th Int. Congr. Blood Transfusion, Lisbon*, 353.
- HORS, P., AND SARANDESES, D. 1951. Séro-anthropologie en Galicie. *4th Int. Congr. Blood Transfusion, Lisbon*, 352.
- LATTES, L., AND GARRASI, G. 1932. Prime ricerche italiane sugli antigeni individuali M ed N; ereditarietà e distribuzione degli antigeni M ed N nella popolazione italiana. *Atti del IV Congresso nazionale di Microbiologia*, 146-150.
- WIENER, A. S. 1931. Heredity of the agglutinogens M and N of Landsteiner and Levine. II. Theoretico-statistical considerations. *J. Immunol.*, 21, 157-170.
- WIENER, A. S. 1935. Heredity of agglutinogens M and N of Landsteiner and Levine; additional theoretico-statistical considerations. *Human Biol.*, 7, 222-239.
- WIENER, A. S. 1943. *Blood Groups and Blood Transfusion*, 3rd ed. C. C. Thomas, Springfield.

HERITABILITY OF SPOT-NUMBER IN SCILLONIAN STRAINS OF
THE MEADOW BROWN BUTTERFLY (*MANIOLA JURTINA*)

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1. DATA

In the first of a long series of papers (which have been summarised by Ford (1964)) on the variability of spot-numbers in *Maniola jurtina*, Dowdeswell and Ford (1952) suggested that the stability of the frequencies of the spot-phenotypes in colonies of this grass-feeding, univoltine insect was maintained over wide areas by selective forces which were independent of considerable differences in climate, soil, etc. Attempts to demonstrate the heritability of

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