

CONCERNING THE INHERITANCE OF RED HAIR

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ALTHOUGH there is little doubt of the hereditary nature of red hair color, the details of the transmission of this trait remain somewhat obscure. It is generally agreed that the factors responsible for black hair are epistatic to those determining red. Even in dark brown haired individuals the detection of red pigment may be difficult. These facts, together with the probable existence of modifiers of the depth of red pigmentation, complicate the study of the inheritance of red hair color. Nevertheless, two main hypotheses have been advanced:

1. The presence of red pigmentation in the hair depends on a dominant factor, *R*, which is inherited independently of the factors determining black or brown hair color (Fischer,^{4,5} Davenport and Davenport³). (However, C. B. Davenport, in a letter to Saller published in part by the latter,⁸ writes that since the publication of his original paper he has collected much additional data and that "usually the red hair acts like a recessive trait but there seem to be many exceptions.")

2. The production of red pigment depends on homozygosity for a recessive factor (Philipschenko and Liepin, 1925, quoted from Saller,⁸ Saller,^{7,8})

Conitzer,² in an extensive treatment and review of this subject, has concluded that the bulk of the evidence favors the first hypothesis, and this viewpoint seems to have gained rather general acceptance.^{1,9}

Now, it is obvious that a decision as to which scheme is more nearly correct can most readily be reached through an analysis of the offspring of marriages involving two red headed people. On the second hypothesis, only red headed children should result from such a union, while on the first there should result something under 25 per cent of non-red headed offspring, with the exact proportion depending on the frequency of the gene in the population. Reports concerning the children of marriages between

red heads are rare, only seven published ones being known to the author. The results of these former reports are summarized in Table I. From this it is obvious only that further data are needed.

Recently I have had the privilege of going through the files of the Genetics Record Office, Carnegie Institution of Washington, at Cold Spring Harbor, L. I., N. Y., and have been able to locate 26 additional reports of fertile marriages between two red headed individuals. It should perhaps be emphasized that the pedigrees have for the most part been sent in to the Record Office by interested people scattered all over the country, so that standardized criteria of redness and investigation of cases by trained investigators have not been possible. Some of these pedigrees probably constitute part of the "additional data" which Davenport referred to in his letter to Saller quoted above. The results of these marriages are summarized in Table II. Among 114 offspring of such unions, 101 were red heads and 13 had hair of some other color. It is unfortunate that in most cases there are no data on the exact hair color of the non-reds. Careful examination of the hair of the non-reds and verification of parentage where possible would have been highly desirable. Be that as it may, if we take the data at face value, the occurrence of so many non-red heads would seem to exclude the hypothesis of simple recessiveness, without, however, necessarily proving hypothesis 1 as stated above. If the factor for red hair is completely dominant, one would expect to find more than 13 non-red headed children among these 114 offspring. This follows from an analysis of gene frequencies.

The proportions of the various hair types in the United States are roughly

as follows (Gould, 1869, quoted from Conitzer,² Trotter¹⁰):

brown and darker (in which red pigmentation would be detected with difficulty or not at all by the untrained observer)	0.575
dark blond and lighter (in which red could usually be detected with no difficulty)	0.400
red	0.025

The proportion of red headed people in the latter two categories, which are the only ones in which the inheritance of red hair can be studied, is 0.059. Assuming, with the first hypothesis, that red is completely dominant, the frequency of the "non-red factor," *r*, is $\sqrt{1.000 - 0.059}$, or 0.97, and of the dominant *R*, 0.03. The frequency of the genotypes *RR*, *Rr*, and *rr*, assuming random mating, is thus approximately 0.001, 0.058, and 0.941. Among the red heads the proportion of *RR* is 0.017, and of *Rr* 0.938, i.e., the heterozygous class is much more common, as is always the case when a rather infrequent factor is involved. Matings between two red heads will be of the following types, with the results noted below.*

For the matings described in Table II the expectation is thus 86.5 red heads and 27.5 non-reds. χ^2 for the difference between observation and expectation is 10.09, which with one degree of freedom has a *P* value much less than 0.01. There is a very real deficiency of non-red headed offspring among the children of these marriages, on the basis of the hypothesis of dominance.

At least two alternate hypotheses concerning the inheritance of the trait appear feasible. One is that the *R* gene is an incomplete recessive which is occasionally penetrant in the heterozygote. A high proportion of the red heads in the population would thus be the homozygous type. Perhaps the heterozygotes tend to be the "sandy reds," in contrast to the clear red homozygote. The other hypothesis is that the red color of the

hair is under the control of either of two different factor pairs. If both of the assumed factors are recessive, then when two red haired people, in whom the genetic basis of the trait differs, marry, they should have some or all non-red headed offspring, depending on their heterozygosity or lack of the alternate factor. Unless one of the two factors is considerably rarer than the other, a high proportion of the marriages might be expected to result in all non-red offspring. Actually, this occurs only once among the 26 marriages, and this in a "family" of one child. If the trait may be due to either a dominant or a recessive factor, then the dominant must be much rarer than the recessive, since otherwise again a higher proportion of marriages between reds would yield non-red headed children.

While a critical decision between these possibilities is not feasible, a further consideration of the data lends some support to the first. If we assume that red hair is the result of a nominally recessive factor which is occasionally pene-

TABLE I. A summary of the offspring of previously reported marriages between two red headed people.

Marriage no.	Total no. of children	No. with red hair	No. without red hair	Investigator
1	3	3	0	Davenport and Davenport (1909)
2	9	0	9	" " *
3	4	1+2?	1?	Rodenwaldt (1927), *quoted from Saller (1931)†
4	1	0	1	Saller (1927)
5	2	2	0	Saller (1931)
6	3	3	0	" "
7	5	5	0	Keers (1932)

*In the light of available data this must be considered an extremely unusual result. Four of the children had black hair; one, brown; three, golden; and one, yellow. The parents had dark red hair.

†One of the children was certainly red haired, two reputedly so, and the reports concerning the fourth were conflicting.

*Mating	Frequency	<i>RR</i>	Offspring <i>RR'</i>	<i>R'R'</i>
<i>RR</i> × <i>RR</i>	0.88 ²	0.7744		
<i>RR</i> × <i>RR'</i>	2 × 0.88 × 0.12	0.1056	0.1056	
<i>RR'</i> × <i>RR'</i>	0.12 ²	0.0036	0.0072	0.0036
		0.8836	0.1128	0.0036

trant in the heterozygote, then the results of Table II could be accounted for by the further assumption that some two per cent of the individuals heterozygous for the red factor possessed red hair. Thus, if we let p equal the frequency of the non-red factor, now designated as R' , and q the frequency of R , then on the assumption of a two per cent penetrance of the erstwhile dominant R , the proportion of non-red headed people among blondes, 0.941 , equals $p^2 + 1.96 pq$, and the proportion of red heads, 0.059 , equals $q^2 + 0.04 pq$. The solution of either of these two equations gives a p value of 0.773 and a q value of 0.227 . Among phenotypic red heads, 0.88 are homozygotes and 0.12 heterozygotes. Random mating would result in the following types of offspring:*

Of the RR' individuals, 0.1105 will be non-red headed, and 0.0023 red headed. The phenotypic ratio will thus be 0.8859 red heads to 0.1141 non-red heads, or, in terms of 114 children, $100.99:13.01$. It is worth emphasizing that when an uncommon recessive factor is involved, even a low penetrance in the heterozygous condition will lead to many exceptions to the recessive rule.

On this assumption of a two per cent penetrance of the factor for red hair when heterozygous, 77 per cent of the marriages between red heads should result in all red headed children. Actually, in the 26 families studied, 69.3 ± 8.6 per cent of the marriages yielded all red heads. If we exclude family 26 , for reasons given in the table, the percentage is 72.0 ± 9.0 . Moreover, in those marriages between a red head and a non-red head or between two non-red heads which yield red headed offspring, there should be a slight excess of red heads over expectation on the hypothesis of complete recessiveness. The data of Saller⁸ suggest that this is the case. How-

ever, among the marriages yielding non-red headed children, the proportion of non-reds should be 0.505 , whereas actually, excluding family 26 , it is 0.343 ± 0.080 .

Summary

From an analysis of the results of 26 marriages between two red headed people, it appears probable that the color of the hair is not determined by a single

TABLE II. A summary of the offspring of marriages between two red headed people as recorded at the Eugenics Record Office.

Marriage no.	Total no. of children	No. with red hair	No. without red hair
1	13	13	0
2	4	4	0
3	5	3	2
4	1	1	0
5	6	4	2
6	2	2	0
7	7	7	0
8	7	7	0
9	3	2	1
10	6	3	3*
11	4	4	0
12	1	1	0
13	1	1	0
14	4	4	0
15	5	5	0
16	1	1	0
17	3	3	0
18	1	1	0
19	6	6	0
20	3	3	0
21	1	0	1
22	4	3	1
23	1	1	0
24	5	5	0
25	10	8	2
26	10	9	1†
114		101	13

*The three non-reds were black haired. This could be a rare case of incomplete epistasis of black over red in the parents and some of the offspring.

†The parents had auburn hair. The first nine children had red hair, while the tenth had brown or black. The latter might have been a young child at the time of the report, in whom detectable red pigment had not yet developed.

*Type	Frequency	RR	Offspring Rr	rr
$RR \times RR$	0.017^2	0.000289		
$RR \times Rr$	$2 \times 0.017 \times 0.983$	0.016711	0.016711	
$Rr \times Rr$	0.983^2	0.241572	0.483145	0.241572
		0.758428		0.241572

completely dominant or recessive factor. Rather, the data are consistent with the hypothesis that the characteristic is dependent upon a single incompletely recessive factor, hypostatic to the factors determining black or dark brown hair color. However, the possibility that all red headedness does not have the same genetic basis and that there are at least two different factors involved cannot be excluded.

Literature Cited

1. BAUER, E., E. FISCHER, and F. LENZ. Human Heredity. Macmillan Co., New York. 1931.
2. CONITZER, H. *Z. f. Morph. u. Anthropol.* 29:83-147. 1931.
3. DAVENPORT, G. C., and C. B. DAVENPORT. *Amer. Nat.* 43:193-211. 1909.
4. FISCHER, E. *Corr.-Bl. der Anthropol. Gesellsch.* 38:141-147. 1907.
5. ———. *Z. f. ind. Abst. u. Vererb.* 54:127-232. 1930.
6. KEERS, M. *Archiv f. Rassen-u. Gesells. Biol.* 27:362-389. 1932.
7. SALLER, K. *Z. f. ind. Abst. u. Vererb.* 45:202-231. 1927.
8. ———. *Z. f. ind. Abst. u. Vererb.* 59:203-219. 1931.
9. SCHEINFELD, A. *You and Heredity.* Frederick A. Stokes Co., New York. 1939.
10. TROTTER, M. *Amer. J. Phys. Anthropol.* 14:433-445. 1930.



TWINS AND SUPER-TWINS

(Continued from page 80)

doubt, and it seems fairly certain that no sextuplets were ever born alive. Among the 60 cases of quintuplets in the literature, some 47 are considered to be authentic. During the past one-and-a-half centuries, four sets have been born in the United States, in 1776, 1800, 1896 and 1936. The 1896 set was born in Kentucky: they lived for some three weeks. With modern baby incubators and the newer nutritional knowledge they might have survived as did the Dionnes. Without either Dr. Dafoe or the necessary machinery, their doom was certain.

Methods of diagnosing one-egg and two-egg twins are discussed at length. The test by the eye alone, whether the twins can be told apart, is probably the best single criterion, with finger and palm prints next. The human eye is able to differentiate an amazing number of human physiognomies, all patterned along remarkably similar lines. The very fact that the eye encounters any difficulty in telling two people apart is strong evidence that a large number of facial features have been integrated, and that no significant differences have been noted. Thus there is good statistical basis for giving the eye an important place as a diagnostic tool. Combined with other elements, such as the blood

groups, finger prints, mirror imaging, etc., few pairs offer any difficulties of classification.

A chapter on twins and human heredity discusses the importance of twins in giving us an insight into the interactions of heredity and environment. The reviewer found this chapter the least satisfactory. The point that twins can be successfully used as an assay of the limits of environmental modification of a great variety of human characteristics perhaps needs more emphasis than it received. This is brought out excellently in citing the contributions twins have made to our knowledge of diseases both mental and physical. The use of twins in the study of mental disease is still only beginning, but already it has considerable promise. The statewide study of twins with tuberculosis and with psychoses now being made by Kallman and others is beginning to bear very promising fruit. It might well have been noted by the author.

The book closes with a review of the twenty cases of identical twins reared apart which were the basis of Dr. Newman's earlier book. The lay reader will get much fascinating information from this unusual book, but he will not get a complete account of research on twins in this and other countries.—R. C.