RED HAIR COLOUR AS A GENETICAL CHARACTER

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INTRODUCTION

Red hair colour has long been considered to be an inherited character, but like other common pigmentary traits in man its mode of inheritance is still obscure. The literature on the nature and inheritance of red hair is confusing and contradictory, and reconciliation of the differences usually is not possible because of the variety of methods used. It will be the purpose of this paper to review briefly the different hypotheses proposed for the inheritance of red hair and then to describe new work done with an improved technique for colour classification.

LITERATURE

It is convenient to present the various hypotheses for the inheritance of red hair in tabular form; this is done in Table 1, listing authors who submit data supporting their statements. A number of workers have proposed hypotheses to explain its heredity but give no supporting data. These include Bateson (1909), Plate (1913), Philipchenko & Liepin (1913, 1925), Hauschild (1926), and Fischer (1930). Scheidt (1925) reported a pedigree which suggested that red hair was dominant over blonde, but he did not draw any conclusions. Since none of these authors propose hypotheses not mentioned in Table 1 they will not be considered further.

Certain criticisms of the data of Table 1 should be made. As will be shown later, the problem of defining what is meant by 'red hair' is one of considerable difficulty. Only three authors used hair-colour standards, and these standards are not the same. Different conceptions of what is red hair, resulting from the lack of a common standard, may help to explain the disagreements between the various hypotheses. Certain specific comments can be made. Davenport & Davenport (1909) present no convincing data for the hypothesis of simple dominance, and other hypotheses appear equally probable. Conitzer (1931) uses against the recessive hypothesis the significantly low segregation proportion of red-haired children, 0·1717, which he finds from the matings of two non-red-haired persons selected for having produced at least one red-haired child. However, he has made an error in his tabulation, and the correct proportion, 0·2073, does not differ significantly from the expected 0·25, assuming simple recessivity. He gives another proportion disagreeing with recessive heredity, but this cannot be checked. Since the correct calculation of the true segregation proportion requires that the data be collected in certain specified ways (Bailey, 1951), and there is some uncertainty about the methods used by Conitzer, there is further doubt about the validity of his conclusions. This last criticism also applies to Saller (1931), who recalculates Conitzer's data. Saller & Maroske (1933) show that when their non-red by non-red and red by non-red matings are pooled the observed number of red-haired children from these matings agrees with the number expected on the hypothesis of simple recessivity. However, if the red by non-red matings are considered separately it is found that the corrected proportion of red-haired children is significantly below 0·5, the value which is expected on a recessive basis. Other criticisms can be made of the remaining four reports in Table 1.

Table 1. *Hypotheses for the inheritance of red hair or red-hair pigment*

Hypothesis	Author	Methods A = colour judged by author O = colour judged by others P = pedigree study	Recorded matings of 2 red-haired persons			Comment
			Matings	Children Red	Non-red	
One dominant autosomal gene	Davenport & Davenport (1909) Conitzer (1931)	A and O, P; no hair colour scale	1	3	0	The Davenports and Conitzer claim dark pigment can hide red pigment when both are present
		A and O, P; segregation proportions; hair-colour scale*	—	—	—	
One recessive autosomal gene	Rodenwalt (1927)	A and O, P; hair-colour scale*	—	—	—	Study of Indonesian half-castes
	Saller (1927)	A, P	—	—	—	Study of Malayans
	Saller (1931)	Segregation proportion; data of Conitzer (1931)	2†	7	0	Recalculated data of Conitzer (1931)
	Saller & Maroske (1933)	A and O, P; segregation proportion; hair-colour scale*	15‡	39	0	—
One autosomal gene, usually hypostatic to a gene determining dark pigment	Keers (1933)	A, P; microscopic examination of all hair specimens; no hair-colour scale	1	5	0	Use of term 'hypostatic' not clear; data seem consistent with recessive hypothesis
One autosomal gene; usually must be homozygous to produce red hair but sometimes may be heterozygous	Neel (1943)	O; segregation proportion; no hair-colour scale	26	101	13§	Data only on matings of two red-haired persons; pooled from many sources

* The three scales are not the same.
† Saller discusses three matings which give non-red-haired children, but believes the data are not reliable.
‡ Families selected to contain at least one red-haired child.
§ In eight families.

Enough has been given to indicate the inconclusiveness of the literature for deciding the method of inheritance of red hair. It is perhaps worth noting, on the positive side, that there seems no doubt that red hair is genetically determined. This is shown by the data on the children of the matings of two red-haired persons. In the literature already cited the great majority of such children are red-haired, often all children in a sibship being red-haired.

METHODS

In order to gain a better understanding of the inheritance of red hair it is desirable to find an objective method of measuring the redness of hair specimens. All previous genetical studies of human hair colour have used the eye for colour judgements, with or without a colour standard. The work of Gardner & MacAdam (1934), who obtained spectrophotometric reflectance curves of hair specimens, showed the possibility of making hair-colour classification more objective. It was decided to use their method to get such reflectance curves for the visible spectrum and to determine redness from measurements of the curves. It would thus seem possible to make a purely physical measurement of colour without any reference to the eye, although the original distinction between 'red' and 'non-red' might still require a subjective judgement.

The Hardy recording spectrophotometer at the National Physical Laboratory, Teddington, was used to make the reflectance curves. This machine automatically draws a curve recording the percentage of reflected light from the specimen being investigated, relative to a magnesium oxide standard, for all wave-lengths from 400 to 700 mμ, that is, the visible spectrum. To insure uniform physical arrangement of hair specimens in the spectrophotometer, the hair from each person was always put into a small paper and cardboard holder. This consisted of two sheets of black paper, one with a circular opening 3 cm. in diameter, between which the hair was placed so that only the circular area of hair was visible, the whole being stapled to a cardboard backing. For uniformity the hair was arranged randomly in the opening and made to lie as flat as possible, projecting hairs being trimmed off.

The following method of gathering and preparing hair specimens was used. All specimens were taken with barber's thinning scissors, thus allowing maximal lengths of hair to be taken without marring the individual's appearance. It is important to avoid taking only the tips of the hairs, since they may change colour relative to the more proximal parts of the hair. When the hair was abundant, specimens were taken about 2 cm. from the scalp in the region of the crown. When less abundant, the hair was cut as necessity dictated. Persons with hair whitened by age were not used, since their hair specimens give no information. Those with only a small proportion of white hairs were used after picking out the white hairs. No specimens were used from hair which showed any signs of having been dyed or coloured. It was usually quite easy to check this point, since the roots of the hairs emerging from the scalp could be inspected while taking the specimen and any colour difference from the rest of the hair noted. All hair specimens were washed twice in ether to remove oil and particles of foreign matter.

Typical reflectance curves for eighteen hair specimens are shown in Fig. 1. Curves 1–9 are of various shades of red and curves 10–18 are shades of non-red hair. It is seen that all curves are rather similar in shape, without maxima or minima, the reflectance increasing with increasing wave-length. The curves for red hair are distinguished from those of non-red hair by having a relatively sharp upturning in the region between 500 and 550 mμ, but as the shade of red approaches brown (curves 4, 2 and 1), this upturning becomes less apparent.
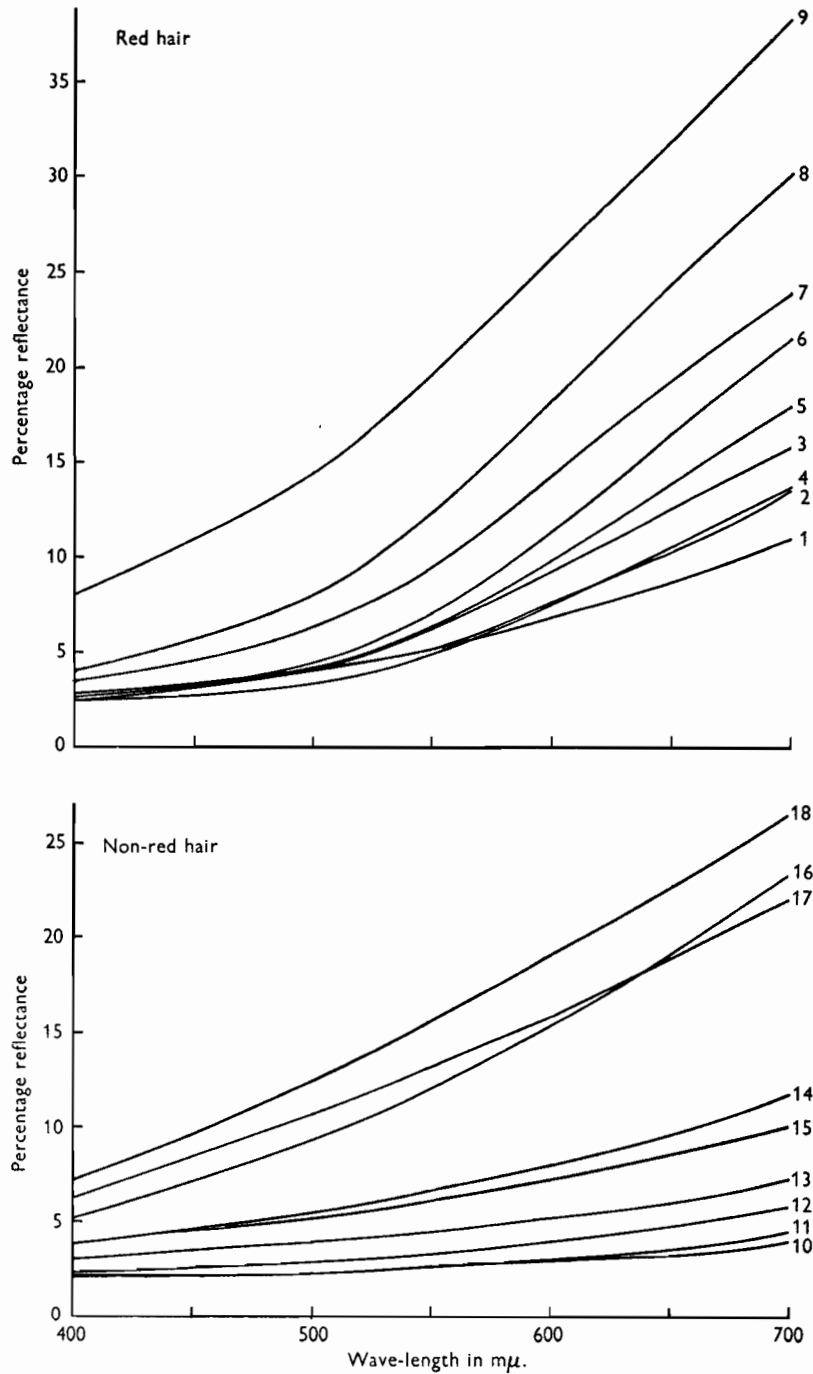
Fig. 1. Reflectance curves of nine red and nine non-red hair specimens.

There are many possible methods for numerically expressing the redness of hair as a function of its reflectance curve. In colorimetry the colour of any object is unambiguously defined by two quantities which are calculated from its reflectance curve in the visible spectrum. However, these numbers are not necessarily the best possible ones for measuring the difference between

phenotypes. Fisher (1936) showed how to obtain the most efficient linear combination of two or more measurements for the purpose of distinguishing between two similar quantities such as plant or animal species. His method is convenient only when the number of measurements is small. Penrose (1947) developed a method for finding the approximate Fisher solution when the number of measurements is large. The efficiency of discrimination can be measured by comparing the square of the difference between the means of the weighted measurements in the two groups with their common variance. In order to test functions of the reflectance curves for discrimination between red and non-red hair, nine red-hair specimens and nine non-red-hair specimens were chosen by eye in daylight, each group containing a very wide range of shades. (The author's own colour discrimination, as shown by the Farnsworth-Munsell 100 Hue Test, is good.) The reflectance curves of these two groups are given in Fig. 1. Values of the reflectances at certain wave-lengths are listed in Table 2.

Table 2. *Reflectance values of nine red and nine non-red hair specimens*

Hair colour	Speci-men no.	Percentage reflectance at indicated wave-length in mμ							
		400	450	500	530	550	600	650	700
Red	1	2·8	3·3	4·0	4·6	5·2	6·8	8·7	10·9
	2	2·4	3·1	3·9	4·6	5·3	7·6	10·3	13·4
	3	2·5	3·1	4·0	5·2	6·1	9·2	12·5	15·7
	4	2·4	2·7	3·3	4·1	4·8	7·4	10·5	13·6
	5	2·6	3·2	4·1	5·2	6·2	9·8	13·9	17·9
	6	2·6	3·2	4·4	5·8	7·0	11·4	16·5	21·4
	7	3·4	4·5	6·3	8·0	9·5	14·3	19·2	23·8
	8	4·0	5·6	8·0	10·3	12·3	18·2	24·5	30·0
	9	8·0	10·9	14·4	17·3	19·5	25·7	31·8	37·4
	Mean	3·41	4·40	5·82	7·23	8·43	12·27	16·43	20·46
Non-red	10	2·2	2·2	2·4	2·5	2·7	3·0	3·3	4·0
	11	2·1	2·2	2·4	2·6	2·7	3·1	3·6	4·5
	12	2·3	2·6	2·9	3·2	3·4	4·0	4·8	5·8
	13	3·0	3·5	4·0	4·3	4·5	5·1	6·0	7·2
	14	3·8	4·6	5·5	6·0	6·6	8·0	9·6	11·7
	15	3·8	4·5	5·2	5·7	6·1	7·2	8·5	10·0
	16	5·2	7·1	9·4	11·0	12·0	15·3	19·1	23·3
	17	6·3	8·5	10·6	12·1	13·1	15·8	18·9	22·0
	18	7·2	9·6	12·4	14·2	15·5	19·0	22·7	26·6
	Mean	3·99	4·98	6·09	6·84	7·40	8·94	10·72	12·79

After many attempts it was found that reflectance values did not give as good discrimination as ratios of reflectance values, this result being in accord with the work of Gardner & MacAdam (1934). The discriminant function finally chosen was found by trial and error to be the best of all the various functions tested, showing the greatest power of discriminating between the two colour groups. If the redness of the specimen is denoted by R then the chosen function is

$$R = \frac{100(y_{530} - 0.243 y_{400})}{y_{650}},$$

where the y subscript is the reflectance at the indicated wave-length. The physical interpretation of this formula is simple if y_{400} is neglected and the curves of Fig. 1 are studied. The red-hair curves have their maximum curvature at about 530 mμ, and most of them have a point of inflexion at about 650 mμ. The non-red curves are in all cases concave upwards with a very

uniform curvature. The ratio of the reflectance at 530 to that at 650 will then act as a discriminant between red and non-red hair, since it is a measure of the characteristic upturning of the curves of red hair. Using the reflectance at 400 mμ increases the discriminating efficiency. The factor 0·243 is found by the method given by Penrose (1947), being α.

The shades of red corresponding to different values of R are roughly as follows:

R	Visual appearance
30–35	Very bright 'copper' red
36–40	Lighter red including red-blonde
41–48	Red brown, approaching brown at higher end.

In general the correspondence with the judgement of the eye seems quite good, the intensity of red increasing with decreasing R. However, the colours corresponding to values of R above 48, approximately, do not show a simple trend. They increase in darkness with increasing R up to a point, then a given R may be either very dark or blonde. The agreement of R with visual judgements was further tested by classifying all of the family hair specimens, to be described later, as 'red' or 'non-red', judging them in daylight in their holders. About 7 % of the specimens are in a region of overlap between the 'red' and 'non-red' distributions, as is shown in Fig. 2. This disagreement does not seem serious considering that the eye may contribute part
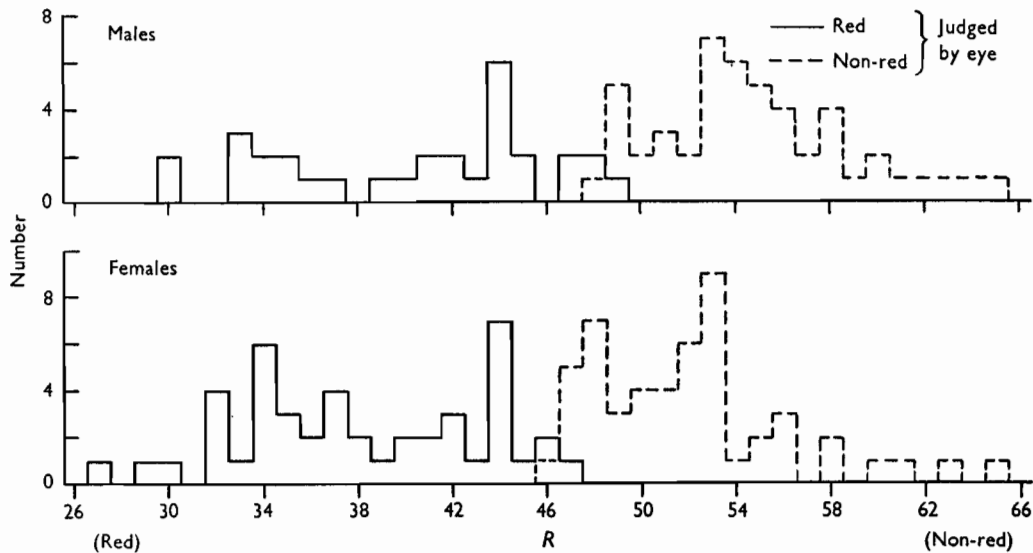
Fig. 2. Distribution of R in thirty-nine families, males, females.

of the error. It is seen that there is no dividing point in the R distribution corresponding to the visual classification, and therefore there seems to be no *a priori* method of distinguishing between red and non-red. If the visual classification is accepted the values of R for red hair are 48 and below for males, 45 and below for females. This difference between the sexes is discussed later.

MATERIAL

In order to investigate the distribution of the R values, and hence the distribution of red hair, in the unrelated and unselected population, small random samples were taken in three different age groups in the London area, 4–8, 20–25 and 36–44 years. Only persons of British ancestry were included. The 4–8 group consists of nineteen boys and nineteen girls from a preparatory

school, the 20–25 group of twenty men and twenty women students from University College and Bedford College, and the 36–44 group of fifteen men and eighteen women high-grade mental defectives from the Harperbury Hospital.

The frequency of red hair in Britain is only about 4 %, and therefore a special effort was made to secure a sufficient number of red hair specimens to study the distribution of shades of red. All children of the Fountain Hospital, London, for mentally defective children, were examined in daylight and hair specimens were taken from all who appeared to have reddish hair. An attempt was made to include all colours which could conceivably be classed as 'red'. Seventeen boys and seventeen girls were selected from a total population of 277 boys and 320 girls, covering an age span of 2–22 years.

Hair specimens were obtained from the children and many of the parents of thirty-nine families in which red hair occurred; each sibship contained from two to seven children, at least one of whom was red-haired. All families but one were of British ancestry and most were from the London area. When parental hair specimens are lacking it is because of either unavailability or whitening of the hair.

RESULTS

The basic data for the three groups of hair specimens are listed in Tables 3, 4 and in the Appendix. In the latter the parents' descriptions of their former hair colour are given, since in many cases the hair colour has changed considerably.

A. Distributions of R

Table 5 shows the distribution of R in the random samples. Only a few bright red-haired individuals occur in these samples; if these are omitted the distribution of the mainly non-red portion seems roughly normal. In Table 6 are shown the distributions for the reddish haired Fountain Hospital population. There seems to be no discernible central tendency in these, perhaps partly due to the small numbers. If the visual standard for redness mentioned previously is accepted, 48 and below for males, 45 and below for females, the frequency of red hair in this population of 597 children is 0.042 ± 0.008. If other standards for redness are used the frequency will vary accordingly. The distribution for the family specimens is given in Fig. 2. In the region of overlap of 'red' and 'non-red' the two distributions are not summed. In both distributions by sex there is a suggestion of bimodality in the 'red' region, but the numbers are too small to make this convincing. The distribution is continuous from bright red to dark brown in the females, and the distribution for the males suggests that this would also be continuous if a larger number were sampled. This indicates that red hair is a non-segregating character as measured by this method.

Fig. 3 compares the distributions of propositi of the sibships, the sibs of the propositi, and a control population of unrelated individuals. In six of the thirty-nine sibships there was no actual propositus, and in these a 'statistical propositus' was obtained by selecting one of the two or more red-haired sibs at random. Individual 9-3 was not used because of the colour change with age. The control population is the combined population of the 4–8 and 20–25 year age groups of the random samples; this approximates the age range of 1–33 years found in the sibships. The distribution indicates that roughly one-third of the sibs of the propositi themselves have red hair of some shade. A statistical summary of the separate male and female distributions is given in Table 7. The variance of the sibs is significantly greater than that of the control

Table 3. *Reflectances and R of three random samples*

Group		Specimen no.	Percentage reflectance at			R
			400 mμ	530 mμ	650 mμ	
4–8 yr.	Males	107	6·7	15·1	26·6	51
		108	3·0	4·2	6·7	52
		109	3·1	6·4	13·7	41
		110	8·4	17·3	27·3	56
		111	2·4	3·2	5·1	51
		112	4·8	9·1	15·2	52
		113	3·0	3·8	5·5	56
		114	4·4	7·2	11·1	55
		115	2·8	3·5	5·1	55
		116	3·4	5·5	9·4	50
		117	3·4	6·1	10·8	49
		118	3·9	6·4	10·2	54
		119	3·7	5·6	9·2	51
		120	8·8	16·0	24·0	58
		121	3·5	5·4	9·2	50
		122	5·1	8·8	13·8	55
		123	7·1	13·4	20·9	56
		124	3·5	6·0	10·2	51
		125	4·6	10·2	18·3	50
	Females	126	2·4	3·2	4·7	55
		127	2·9	6·0	12·1	44
		128	2·9	4·6	7·7	51
		129	5·5	10·8	18·3	52
		130	2·5	4·4	7·5	51
		131	2·5	4·0	6·5	52
		132	2·0	2·5	3·8	53
		133	2·1	3·2	5·6	48
		134	3·2	6·0	10·2	51
		135	3·5	6·7	11·2	53
		136	3·5	6·5	11·0	52
		137	5·5	11·5	19·2	53
		138	9·9	22·6	32·5	62
		139	2·7	3·7	5·5	55
		140	2·4	4·0	7·4	46
		141	3·6	7·8	14·5	47
		142	2·6	4·5	7·5	52
		143	9·0	17·4	26·1	58
		144	3·4	8·5	18·7	41
20–25 yr.	Males	1	7·0	13·0	19·7	57
		2	2·8	5·5	9·2	52
		3	2·5	4·1	6·5	54
		4	4·2	8·5	13·8	54
		5	2·0	2·8	3·8	61
		6	2·2	2·8	3·9	59
		7	2·8	4·3	7·0	52
		8	2·4	3·2	4·7	55
		9	2·6	3·9	6·5	51
		10	4·8	9·9	16·0	54
		11	3·0	4·3	6·9	52
		12	2·8	3·9	5·6	57
		13	3·2	5·0	8·0	52
		14	2·9	3·7	5·0	60
		15	2·7	3·8	5·5	56
		16	2·1	3·3	5·0	56
		17	2·7	3·9	6·0	53
		18	2·3	3·7	7·0	44
		19	2·5	3·1	4·6	54
		20	2·2	3·3	5·5	51

Table 3 (*continued*)

Group		Specimen no.	Percentage reflectance at			R
			400 mμ	530 mμ	650 mμ	
20–25 yr.	Females	21	2·9	4·3	7·2	50
		22	2·5	4·3	7·8	47
		23	3·7	5·5	8·5	54
		24	2·5	3·9	6·6	50
		25	2·2	2·8	4·5	51
		26	2·9	6·1	14·0	39
		27	3·0	6·6	15·6	38
		28	3·8	8·0	14·5	49
		29	2·6	4·2	6·9	52
		30	2·2	3·2	5·1	53
		31	2·4	3·5	6·1	48
		32	2·6	3·9	6·7	49
		33	2·3	2·9	4·2	55
		34	2·6	3·6	5·8	52
		35	2·4	3·0	4·0	60
		36	3·2	5·2	8·8	50
		37	4·5	9·4	16·3	51
		38	3·2	5·6	9·7	49
		39	2·8	4·1	6·9	49
		40	2·0	2·9	4·4	55
36–44 yr.	Males	86	3·1	3·8	5·3	57
		87	4·2	6·6	9·7	58
		89	3·0	4·5	6·7	57
		90	2·4	3·2	4·3	61
		91	2·2	3·9	6·3	54
		92	2·0	2·6	3·4	62
		93	2·7	4·9	9·5	44
		94	1·8	2·9	4·2	60
		95	3·7	8·5	14·5	52
		96	2·7	4·0	7·0	47
		97	2·3	5·1	9·6	47
		98	2·0	3·0	4·5	56
		99	2·1	3·3	4·8	58
		100	1·9	2·7	4·0	55
		106	3·0	4·6	7·2	54
	Females	65	3·6	6·6	12·5	46
		66	1·9	2·6	4·0	52
		67	2·5	3·5	6·0	48
		68	3·0	4·4	6·8	54
		69	2·4	2·9	4·0	58
		70	4·0	9·8	17·4	50
		71	2·4	3·8	5·8	55
		72	2·6	5·8	11·6	45
		73	1·8	3·4	6·1	49
		74	3·9	6·5	10·8	52
		75	2·3	3·4	5·7	49
		76	2·7	4·5	7·6	50
		77	1·9	2·5	3·5	57
		79	3·5	4·5	6·7	55
		80	2·5	3·3	5·2	52

	4–8 yr.		20–25 yr.		36–44 yr.	
	Males	Females	Males	Females	Males	Females
Number	19	19	20	20	15	18
Mean of R	52·26	51·37	54·20	50·05	54·80	51·83
Standard deviation of R	3·80	4·80	3·78	4·96	5·32	3·71
Standard error	0·87	1·10	0·85	1·11	1·37	0·87

Table 4. *Reflectances and R in a reddish haired population*

Specimen no.	Sex	Age*	Percentage reflectance at			R
			400 mμ	530 mμ	650 mμ	
D7	Male	2	3·4	8·0	19·2	37
F1		3	4·8	8·5	14·8	49
D8		3	4·0	10·3	24·5	38
F2		5	3·4	7·3	16·5	39
F3		5	3·4	7·1	16·0	39
D5		6	2·6	5·2	13·9	33
F4		7	4·1	8·1	16·1	44
D9		8	8·0	17·3	31·8	48
F5		9	4·5	9·0	18·0	44
F6		9	5·3	10·6	18·6	50
F7		11	3·1	5·1	10·3	42
F8		12	3·5	6·5	13·2	43
F9		13	2·6	3·6	6·0	50
F10		13	2·0	3·0	5·4	46
D1		14	2·8	4·6	8·7	45
F11		14	3·7	7·0	13·6	45
F12		15	3·7	7·0	13·5	45
F13	Female	5	4·4	9·0	16·3	48
F14		5	4·4	10·1	19·7	46
D6		6	2·6	5·8	16·5	31
F15		7	3·5	8·7	19·7	40
F16		9	2·4	4·5	10·9	36
F17		11	3·0	6·4	15·0	38
F18		11	3·5	6·6	12·4	47
F19		13	2·4	4·8	10·1	42
F20		13	2·6	4·1	7·5	47
F21		14	3·0	6·4	15·3	37
F22		15	3·8	8·1	15·2	47
F23		15	3·8	7·6	13·6	49
F24		16	3·1	6·5	14·0	41
F25		17	2·3	4·3	9·5	39
F26		17	4·0	8·5	17·2	44
F27		19	2·7	4·9	10·0	42
F28		22	2·5	5·1	12·3	37

	Males	Females
Number	17	17
Mean of R	43·35	41·82
Standard deviation of R	4·84	5·10
Standard error	1·17	1·24

* To the nearest year.

Table 5. *Distribution of R in three random samples*

R	No. in R interval					
	4–8 years		20–25 years		36–44 years	
	Males	Females	Males	Females	Males	Females
38–41	1	1	0	2	0	0
42–45	0	1	1	0	1	1
46–49	1	3	0	6	2	4
50–53	9	10	7	8	1	7
54–57	7	2	9	3	6	5
58–61	1	1	3	1	4	1
62–65	0	1	0	0	1	0

population, and the mean of sibs is significantly lower. This last result is evidence for the genetical determination of red hair.

Most of the thirty-nine sibships can be classified into one of three groups, according to whether neither, one, or both of the parents report having had red hair. The distribution of R within

Table 6. *Distribution of R in a reddish haired population*

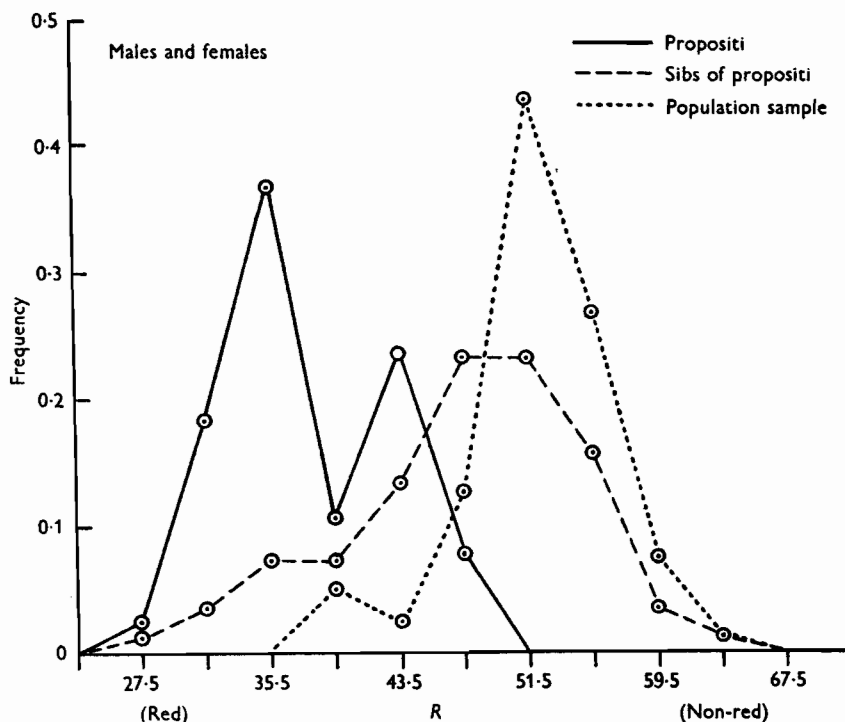| R	No. in R interval	
	Males	Females
30–31	0	1
32–33	1	0
34–35	0	0
36–37	1	3
38–39	3	2
40–41	0	2
42–43	2	2
44–45	5	1
46–47	1	4
48–49	2	2
50–51	2	0

Fig. 3. Distribution of R in red-haired propositi, sibs of propositi, and a population sample (4–8 and 20–25 year random samples).

sibships so classified is given in Fig. 4. Sibships in which the father has a red beard or moustache and non-red scalp hair were not used, nor were sibships nos. 14, 29, and 34, because of doubtful colour classification. Sibship no. 9 was not used because of the age change in colour of individual 9-3. The details of these distributions are given in Table 8. The most striking result is that all

ten children from the four matings of two red-haired persons have red hair. (There is another child from sibship no. 1 who has red hair but is not represented.) Within some sibships there is evidence for segregation into distinct colour groups, especially in sibship no. 2, but sibship totals give no evidence for segregation. In interpreting the significant differences found between the means of the different distributions, it should be remembered that if red hair is determined by one or two genes the effect of chance gene segregation would be such as to make it likely that

Table 7. *Comparison of propositi, sibs of propositi, and a population sample*
(4–8 year plus 20–25 year random samples)

	Males			Females		
	Propositi	Sibs of propositi	Population	Propositi	Sibs of propositi	Population
Number	16	39	39	22	43	39
Mean R	38·75	49·56	53·26	37·09	46·19	50·69
Standard deviation	5·93	6·92	3·86	4·96	7·69	4·86
Standard error	1·48	1·11	0·62	1·06	1·17	0·78

Variance ratio

	Males	Females
V(sibs of prop.)/V(population)	3·21	2·50
Probability that the difference in variance is due to chance	<0·002	<0·02

Difference in mean R between the sibs of propositi and population sample

	Males	Females
Difference in mean R	3·70	4·50
*Probability that the difference in mean is due to chance	<0·02	<0·02

* Using method of Aspin (1949).

there would occasionally be significant differences between the means of different groups of children even when the parents have the same genetical constitution. The significant difference between means of males and females from non-red by non-red parents may be an example of this. It seems, however, that the hair of children of two red-haired parents is significantly redder than the hair of children from other matings, this being the case for three of the four possible like-sex comparisons. An analysis of variance of the three distributions shows that for each mating type the variance between sibships is not significantly greater than the variance within sibships, at the 0·05 level of significance, and therefore the means of the different sibships do not differ significantly from each other. None of the three variances within sibships differs significantly from any other, although if there were more data on matings of two red-haired persons showing the same trend as the present data, the children from these matings would show significantly less variation than the children of the other two matings.
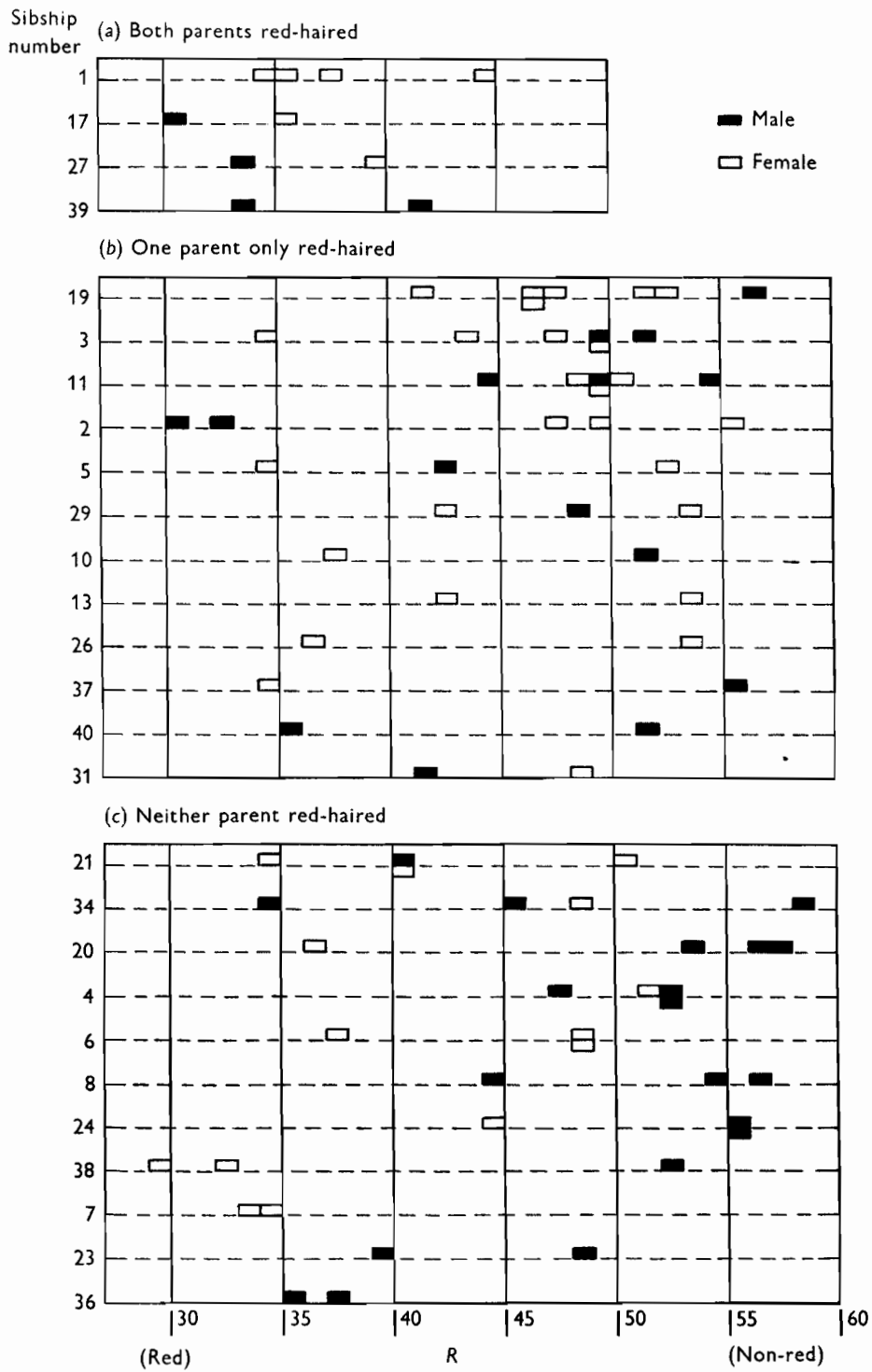
Fig. 4. Distribution of R within sibships. (a) both parents red-haired; (b) one parent only red-haired; (c) neither parent red-haired.

Table 8. *Comparison of the children from three mating types: neither parent red-haired, one parent red-haired, and both parents red-haired.*

Using parents' reports of former hair colour. Families in which the father has a red beard or moustache and non-red scalp hair are not included, nor is family 9.

	Children from the indicated mating					
	Red × Red		Red × Non-red		Non-red × Non-red	
	Males	Females	Males	Females	Males	Females
Number	4	6	15	27	20	14
Mean R	34·3	37·3	45·87	45·85	48·45	40·29
Standard deviation	4·72	3·72	8·28	6·38	7·84	7·64
Standard error	2·36	1·52	2·14	1·23	1·75	2·04

*Significant differences in means**

R = red-haired parent, N = non-red-haired parent.

Between	Probability that the difference is due to chance
$N \times N$ males and $N \times N$ females	< 0·01
$R \times R$ males and $R \times N$ males	< 0·02
$R \times R$ males and $N \times N$ males	< 0·01
$R \times R$ females and $R \times N$ females	< 0·01
$R \times N$ females and $N \times N$ females	< 0·02

* At the 0·05 level of significance.

B. *Effect of sex on redness*

The difference between males and females in mean R value is given for all data in Table 9, together with the probability that this difference is due to chance. It should be remembered that the random population samples consist mainly of non-red specimens, while the reddish hair

Table 9. *Sex differences in mean R*

Group	$\bar{R}_m - \bar{R}_f$	Probability that difference is due to chance
Random samples:		
4–8 yr.	0·89	> 0·30
20–25 yr.	4·15	< 0·01
36–44 yr.	2·97	0·07
Reddish hair specimens	1·53	> 0·30
*Family data, all ages:		
Red-haired only	2·25	0·09
Non-red-haired only	2·74	< 0·01
All specimens	3·28	0·01
< 31 years:		
Red-haired only	1·86	> 0·10
Non-red-haired only	1·73	> 0·10
All specimens	2·57	> 0·10

* The first five consecutive female propositi were removed, so that there are fourteen propositi of each sex.

group is mainly, but not entirely, red-haired according to the previously mentioned standard. To minimize the effect of selection for red hair the numbers of propositi of each sex in the family data have been made equal. It is seen that the only groups showing significant sex differences are entirely or mainly non-red-haired and in older age groups. However, it is note-worthy that in every group the mean R of the females is lower than that of the males. Although these differences are small they indicate that the male distribution of R should not be pooled with the female distribution when a combined distribution is desired. A coarse grouping interval will reduce the effect of sex differences.

C. *Effect of age on redness*

The random population samples show no significant differences between the means of different age groups of the same sex or of both sexes together. The reddish hair specimens are too few and too evenly distributed in time to be of use. If the linear regression of R on age is computed for the family data, the specimens being grouped both by sex and by being 'red' or 'non-red', it is found that the only group which shows a significant regression is that of the 'non-red' males, the regression constant being $0 \cdot 0852 \pm 0 \cdot 0363$ R/year, with a probability of $0 \cdot 02$ of being due to chance. More comprehensive groupings of the data produce no significant regressions.
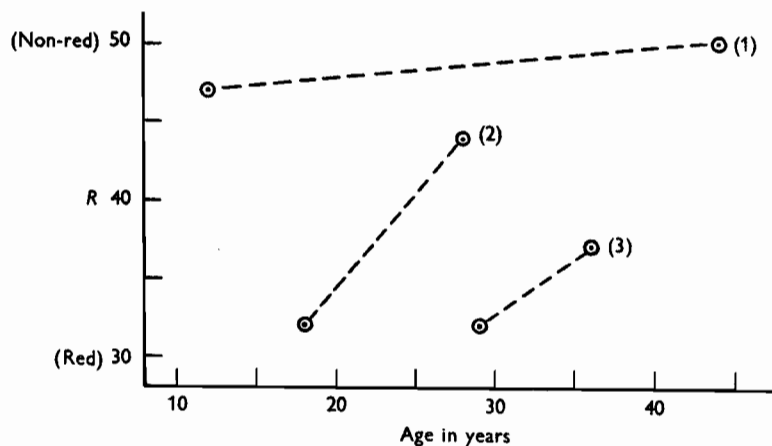

Fig. 5. Age changes in R in three persons. 1. Specimens not used elsewhere. Coordinates 12, 47 and 44, 50. 2. Specimens 9-3 and 9-3E. 3. Specimens 27-2 and 27-2E.

The most satisfactory method of studying the effect of age on R is to follow the individual colour changes of a group of people over a long period of time, or to compare hair specimens taken at different ages. Only three persons were found who had kept hair specimens taken years earlier, one non-red-haired and two originally bright red-haired. Their R and age values are plotted in Fig. 5. These three persons clearly show an increase in R with age, indicating decrease in redness, as was found above, but the rate of increase is quite variable, ranging from $0 \cdot 094$ R/year to $1 \cdot 20$ R/year. This suggests that a simple correction for the effect of age is not feasible.

D. *Sib-sib correlation in R value*

There are two different methods available for calculating the sib-sib correlation. One is to use the data of the thirty-nine sibships in a sib-sib correlation table to find the correlation existing in the data. This correlation, however, will not be that of the general population, which

is what is usually meant by sib-sib correlation, because the data have been selected so that each sibship contains at least one red-haired member. Since the precise statistical method of ascertainment of a number of families is not known, being obtained indirectly, it is not possible to correct for this selection and so obtain an estimate for the unselected population. The other method, which should give an estimate of the sib-sib correlation in the general population, makes use of the means of the propositi, sibs of propositi, and the general population, whose values are given in Table 7. If the values of these three means are, respectively, a, b and c, the expression $(c-b)/(c-a)$ is an estimate of the correlation. The value of the correlation obtained by the first method, calculated from the separate brother-brother, sister-sister and brother-sister correlations, which do not differ significantly from each other, and the two correlations using the second method, one from males and one from females, are listed in Table 10. It is seen that the correlations are small, 0·26–0·33, but significant, and therefore the R value is at least partly determined by heredity. The genetical determination of red hair cannot be clearly demonstrated by these correlations, since some correlation can arise because of similarity in non-red shades of colour.

Table 10. *Estimates of the sib-sib correlation in R value in the data and in the general population*

Method and type of estimation	Correlation coefficient	Probability of being due to chance
Correlation table—estimates correlation in sibship data, not in general population	0·26	<0·001
Regression of sibs of propositi on propositi as calculated from the three means of Table 7—estimates correlation in general population:		
Males	0·26	<0·01
Females	0·33	<0·001

E. *Sib-sib R difference*

Another procedure for examining the behaviour of the R values is to find the distribution of the differences in R within sib pairs. Only like sex pairs were used because of the sex difference in mean R demonstrated in part of the data, and in order to reduce ambiguity caused by the variety of non-red colours the distribution of R values less than 53 has been given as well as that of all R values. These distributions are shown in Table 11. In spite of the prominent peaks the small numbers make it impossible to show that any of them are significant, using the method of Haldane (1952).

F. *Parents' mating type and R of reddest child*

If the sibships are classified by the R value of the reddest sib and by whether neither parent or at least one parent reports having had red hair, a relationship between redness of parents and redness of children may be looked for. It was found that although the sibships with redder sibs tended to have a higher proportion of parents with some red hair than sibships with less red sibs, this tendency is not significant. Inheritance of the degree of redness therefore cannot be shown.

G. *Use of parents' R values*

No critical use has been made of the parents' R values because of evidence of fading with age. Eighteen parents whose hair specimens were usable described themselves unequivocably as having had red hair in their youth. Of these, twelve have R values which by the eye standard for red hair previously mentioned, 45 and below for women, 48 and below for men, were nonred, including seven with values of 50 or more. There has been considerable fading in redness in these specimens, and the present R value does not give a reliable indication of the former hair colour.

Table 11. *Distribution of sib pair R differences in like sex pairs*

R difference	$R \leqslant 52$	All R	R difference	$R \leqslant 52$	All R
0	4	5	17	0	1
1	7	9	18	1	1
2	8	8	19	0	0
3	3	4	20	0	0
4	3	5	21	0	0
5	9	10	22	0	0
6	7	8	23	0	0
7	1	1	24	0	1
8	1	2	25	0	0
9	4	4	26	0	0
10	4	7	27	0	0
11	5	6	28	0	0
12	1	3	29	0	1
13	1	2	30	0	0
14	0	0	31	0	0
15	1	1	32	0	0
16	2	2	33	0	1

H. *Determination of redness by R value*

The distributions of R in the various data show that the use of R values provides no *a priori* method for distinguishing red hair from non-red, the values of R showing a continuous distribution from bright red to black or white. A visual standard for redness can be defined, as has been done, but this does not eliminate subjectivity from the problem of distinguishing red from non-red. In connexion with this point a small amount of microscopy of family hair specimens was done, using the Hardy thin cross-section device (Hardy, 1935). This sections about 150 hairs at a time and provides a simple method of examining in cross-section a large number of hairs from a single specimen. Microscopic examinations were made of hair specimens of ten individuals, in three sibships, who are sibs of red-haired persons but are themselves non-red both in appearance and in R value. Six of the ten had at least one hair with definite red granules; some had a number of reddish hairs. Specimen 2-7 was the most striking, having about one-fifth of the hairs with red granules and an R value of 55. It appears that the spectrophotometer and the unaided eye have similar limitations, both being unable to detect very small amounts of red pigment. Keers (1933) has also made this observation. From these facts it appears that red hair, as observed by the unaided eye or measured spectrophotometrically, is a continuous character and does not segregate from non-red hair. It seems improbable that accurate genetical studies on red hair can be made using these macroscopic methods.

Discussion

In trying to devise a more objective method for measuring the degree of redness of hair specimens it becomes clear that a certain amount of subjectivity cannot be eliminated when dealing with the less conspicuous shades of red, since visual judgements about these must be made in the process of making a colour discriminant. However, study of the spectrophotometric reflectance curves of many different hair specimens shows such a basic similarity of shape between the very bright red shades and the less bright, with a gradual transition to the shape of the definitely non-red, that one can feel confidence in using a function which expresses the degree of similarity between any curve and that of a bright red hair specimen. The discriminant function chosen does this, being primarily a measure of the characteristic upturning of the curves of bright red hair in the green region of the spectrum. Agreement between numerical values of the function and the eye seems quite good for various shades of red, but among non-red colours there is a certain amount of ambiguity, since a black specimen and a blonde specimen may have the same value. As the main purpose of the function is to indicate degrees of redness this behaviour was not considered serious, and in practice the small proportion of blonde hair specimens made this ambiguity unimportant.

The small but significant sex difference in mean R value found in several mainly or entirely non-red-haired populations was unexpected, and the reason for it is not known. These sex differences indicate that in these populations females are nearer to being red-haired than males, without, in most instances, actually being red-haired. The possibility that this is due to hair washes and tints cannot be ruled out, although no obviously dyed hair was used. The greater hair length in females, resulting in greater exposure of the hair tips, may be a factor, since it appears that the ends of hairs tend to redden with respect to the rest of the hair (Scheffelt, 1915; Keers, 1933; Saller & Maroske, 1933), apparently as a result of exposure. In collecting hair specimens for the present study it was noticed that quite often in weakly red hair the front areas of the head, most exposed to sunlight, were much redder than the less exposed parts. Another possibility is that the sex hormones may produce a difference. It is known that they can strongly influence non-red pigmentation (Hamilton & Hubert, 1939; Hamilton, 1948).

Several results give evidence for the genetical determination of red hair without suggesting the type of inheritance. The significant sib-sib correlation coefficients are evidence for the genetical determination of the R value, but not necessarily of red hair, since the R value measures non-red colour variation also. The data are not extensive enough to divide into 'red' and 'non-red' groups. The significantly lower mean R of the sibs of propositi, compared with that of the control population, does indicate that red hair is genetically determined. Moreover, the eleven children of the four pairs of parents who were both red-haired in their youth all have red hair. (One child in family no. 1 is not in the data.) The similarity of R values in the two red-haired identical-twin pairs also indicates genetical determination. These facts of themselves tell nothing about the mode of inheritance involved.

The fact that the only significant regression of R on age was found in the 'non-red' males seems strange, since it is known that red hair darkens with age. If the effect of age on redness were no more than the regression data indicate it would be negligible, but the direct evidence of changes of colour with age in three persons shows that it can be important. Two of these persons had bright red hair, and their rates of change of redness, as shown in Fig. 5, are 0·71 R/year and 1·20 R/year. The latter rate produced quite a striking change in 10 years, resulting

in a dark red-brown colour. How typical these values are is not known; it is known that some bright red hair darkens more slowly, as shown by the R values in the family data. The present non-redness of a number of the parents who claimed to have red hair in their youth also indicates the prevalence of fading. These facts make it difficult to have any confidence in measurements of the redness of parents or in accurate comparisons of parents with their children. This property of red hair is a considerable detriment to its usefulness as a genetical marker. A more extreme example of fading is occasionally encountered in persons who have been born with red hair but have this replaced in a few years by non-red hair; several such individuals were seen by the author. Fortunately, this occurrence is not common.

The most important results of this study concern the segregation and identification of red hair. Some of the individual sibships were seen to show a definite segregation into red and non-red hair colours, but many did not, and the sibship totals for the different mating types did not. The distribution of R for all family data also showed no segregation into colour types, showing instead a continuous distribution from bright red to the various types of non-red. Study of the original reflectance curves makes it clear that this continuity is a consequence of the smooth transition in shapes of the curves in going from one colour to another. The limited information from microscopy indicates that macroscopic examination of hair, either by eye or by reflectance curves, cannot detect very small amounts of red pigment, and suggests that the continuous distribution of redness is partly due to the widely varying proportions of red pigment, out of all pigment, which may be found in different hair specimens. Since one specimen with an R value of 55 was found to have red pigment present microscopically, it may be seen from the distribution of R values in the family data that it is possible for a considerable proportion of the macroscopically 'non-red' hair specimens to be misclassified. Microscopic examination of a large number of hairs from each individual would improve the discrimination between hair specimens containing red pigment and those lacking it, but even this method has defects, since it is not uncommon to find hair with pigment granules whose colour cannot be decided. Because no segregation into 'red' and 'non-red' could be shown, no segregation proportions were found in the family data, and thus no statistical tests of hypotheses for the inheritance of red hair were made. In view of the contradictory state of the literature, it seems desirable that further work on red hair inheritance should attempt to find out whether a sharper distinction between 'red' and 'non-red' is possible.

The prevalence of non-genetical variation in redness is another difficulty for accurate classification. The change of colour with time has already been discussed, but the change with location on the body is also important. It is quite common among the weakly red-haired persons to find that adjacent areas of the scalp have hair of different colours. A representative hair specimen is difficult to secure in such cases. Specimens having 1 or 2 % of the hairs bright red and the rest non-red are another common example of this difficulty, as are the cases of non-red scalp hair and red beard.

The disagreements of the literature on red hair heredity, as summarized in Table 1, become more understandable in the light of these results. All authors but Keers depended on macroscopic colour judgements, and it seems probable that their definitions of what constituted red hair differed. Some of the more critical data are further complicated by incorrect statistical procedures, including the method of ascertaining the data. At the present time the data on the children of two red-haired persons seem to be the most satisfactory, partly because they provide

a critical test for the recessive hypothesis. The four such matings of the present study, as well as most of the matings listed by the authors of Table 1, show that all of the children are red-haired, but Neel's data show eight out of twenty-six matings producing a non-red-haired child. Although his data are collected at second-hand and do not seem as reliable as one would like, it appears that perfect recessivity does not adequately explain the heredity of red hair. His hypothesis that red hair usually appears in persons homozygous for a certain gene, but occasionally does so in heterozygotes, provides a simple formal explanation of the observed facts. If the heterozygotes are usually more weakly red than the homozygotes and include most of the persons having only a few red hairs among many non-red hairs, this hypothesis helps to explain facts about the various degrees of red-hairedness. In persons of northern European ancestry the presence of a few red hairs is not uncommon; Michelson (1934) found that 18 % of American white males had one or more red hairs, although the frequency of 'red hair' in the population is of the order of 2 %. The above supposition would account for the relatively high figure of 18 %, since the heterozygotes are expected to be much more numerous than the homozygotes. Such a variable manifestation of red hair does not seem so unusual when one considers that it is probable that there are many genes affecting hair colour, this being the case in all intensively studied mammals. The mouse, for example, has at least fifteen genes determining hair pigmentation (Grüneberg, 1952). Interaction between the effects of different genes is common, and this may affect the degree of dominance of a gene. In the mouse the spotting effects of 'dominant spotting' and 'microphthalmia' illustrate this, on some genetical backgrounds behaving as dominant genes, on others as recessive. It is seen, therefore, that there is some precedent for Neel's hypothesis.

This study has not furthered our knowledge of the inheritance of red hair, but instead, by using a different technique, has emphasized the shortcomings of the methods, including the present one, used in studying its heredity. Until better methods of classifying red hair are available, it would seem advisable to use red hair as a genetical character with caution and to consider its mode of inheritance still uncertain.

SUMMARY

The mode of inheritance of red hair is uncertain. A method of numerical representation of degree of redness, based on spectrophotometric reflectance curves, is developed and applied to a variety of hair specimens, including specimens from thirty-nine families containing red hair. Red hair is genetically determined, but, using macroscopic methods, does not segregate from non-red hair. For this reason a better method for classifying red hair is needed in order to use it as a genetical character.

APPENDIX
Family data

Specimen number (grouped by family) -1 = father -2 = mother -3 etc. = children	Sex	Age†	Reflectance % at			R	Parents' former hair colour. r = red-haired n = non-red-haired b = beard or moustache red, scalp hair not red.
			400 mμ	530 mμ	650 mμ		
1-1	m.	55	5·1	8·2	12·9	54	r
2	f.	32	2·1	3·8	11·1	30	r
3	f.	10	2·4	5·1	13·0	35	
*4T	f.	8	2·7	6·0	15·6	34	
5	f.	8	3·0	6·3	15·8	35	
6	f.	6	3·1	8·3	20·5	37	
	f.	4	4·7	13·6	28·6	44	
2-1	m.	45	3·4	6·1	12·6	42	r
2	f.	48	3·3	4·4	6·6	55	n
3	f.	20	3·5	6·1	11·3	47	
4	f.	19	2·6	4·5	8·0	49	
5	m.	14	3·1	6·2	17·7	30	
6	m.	11	3·2	6·4	17·5	32	
7	f.	7	5·5	12·0	19·6	55	
3-1	m.	53	3·8	6·0	10·5	49	r
2	f.	—	—	—	—	—	n
3	f.	20	2·4	3·3	5·8	47	
4	f.	19	2·6	5·4	14·1	34	
5	m.	16	2·6	3·2	5·1	51	
6	f.	15	3·4	7·0	14·3	43	
7	m.	14	3·9	7·7	14·0	49	
8	f.	12	2·5	4·0	7·0	49	
4-1	m.	38	2·6	3·5	5·7	51	n
2	f.	37	3·0	4·3	6·6	55	n
3	m.	13	4·6	9·3	17·6	47	
4	m.	11	4·0	7·4	12·4	52	
5	f.	8	6·0	14·0	24·5	51	
6	m.	7	4·2	7·7	12·8	52	
5-1	m.	59	3·7	4·5	5·7	63	n
2	f.	—	—	—	—	—	r
3	m.	30	3·0	5·4	11·1	42	
4	f.	20	4·0	5·9	9·4	52	
5	f.	17	3·1	6·0	15·3	34	
6-1	m.	53	3·7	5·2	8·1	53	n
2	f.	—	—	—	—	—	n
3	f.	25	3·6	7·8	18·4	37	
4	f.	22	2·5	3·7	6·4	48	
5	f.	13	3·1	4·1	6·9	48	
7-1	m.	44	3·1	4·2	6·3	54	n
2	f.	43	2·8	4·5	8·0	47	n
3	f.	16	2·7	6·2	16·5	33	
4	f.	12	2·7	5·6	14·5	34	
*4T	f.	12	2·7	6·2	16·3	34	
8-1	m.	44	3·8	4·5	5·5	65	n
2	f.	43	5·9	11·2	18·6	53	n
3	m.	12	4·0	8·0	15·9	44	
4	m.	7	4·1	7·0	10·8	56	
5	m.	3	4·9	9·4	15·3	54	

* T = identical twin of preceding person, not used in calculation. E = earlier specimen of preceding person, not used in calculation. † To the nearest year.

APPENDIX (*continued*)

Specimen number (grouped by family) -1 = father -2 = mother -3 etc. = children	Sex	Age†	Reflectance % at			R	Parents' former hair colour. r = red-haired n = non-red-haired b = beard or moustache red, scalp hair not red.
			400 mµ	530 mµ	650 mµ		
9-1	m.	57	3·0	4·0	6·2	53	r
2	f.	49	2·3	3·0	4·8	50	n
3	f.	28	3·8	7·9	15·8	44	
*3 E	f.	18	2·3	5·3	14·7	32	
4	m.	25	4·0	7·7	14·9	45	
10-1	m.	41	3·9	5·9	9·4	53	r
2	f.	41	5·1	9·0	14·6	53	n.
3	m.	15	5·0	10·2	17·5	51	
4	f.	4	3·5	7·9	19·2	37	
11-1	m.	49	3·5	6·6	11·7	50	r
2	f.	47	2·2	3·0	4·5	56	n
3	f.	26	4·5	9·5	17·6	48	
4	m.	24	4·2	8·4	15·2	49	
5	f.	21	4·8	9·3	16·5	49	
6	m.	17	3·3	5·7	9·0	54	
7	m.	15	4·7	10·7	21·6	44	
8	f.	10	4·8	9·8	17·1	50	
12-1	m.	32	2·9	4·1	6·9	49	b
2	f.	36	2·3	4·0	8·5	40	r
3	m.	10	3·1	5·2	10·0	44	
4	f.	8	2·8	6·7	15·6	38	
5	f.	6	3·1	5·9	10·9	47	
6	m.	4	2·9	5·2	10·2	44	
13-1	m.	52	2·9	5·0	7·2	60	n
2	f.	45	4·1	8·5	14·8	50	r
3	f.	12	4·2	11·3	24·3	42	
4	f.	5	4·6	9·3	15·5	53	
14-1	m.	49	2·3	2·8	3·8	58	n
2	f.	46	3·0	5·5	9·5	51	?r
3	m.	22	3·2	5·2	8·9	49	
4	f.	21	2·0	3·8	10·2	32	
5	f.	17	3·0	5·6	11·2	44	
6	m.	13	3·0	5·5	11·0	44	
7	f.	10	3·5	8·0	17·3	42	
8	f.	5	3·7	9·7	23·0	38	
15-1	m.	34	3·4	4·9	7·0	59	b
2	f.	35	2·9	5·5	10·0	48	n
3	m.	10	4·4	8·6	14·1	53	
4	f.	8	2·6	6·9	19·8	32	
5	f.	5	10·5	21·6	31·3	61	
6	f.	2	12·5	25·1	34·0	65	
16-1	m.	39	2·0	2·3	3·1	58	?
2	f.	32	4·0	6·8	11·8	49	?
3	f.	9	3·9	9·0	18·0	45	
4	m.	8	3·5	7·3	15·2	43	
5	m.	4	3·2	4·8	7·5	53	
17-1	m.	32	3·5	7·9	15·0	47	r
2	f.	32	2·4	3·5	5·7	51	r
3	f.	10	2·7	6·0	15·1	35	
4	m.	6	2·0	4·4	13·2	30	

* T = identical twin of preceding person, not used in calculation. E = earlier specimen of preceding person, not used in calculation.   † To the nearest year.

Specimen number (grouped by family) -1 = father -2 = mother -3 etc. = children	Sex	Age†	Reflectance % at			R	Parents' former hair colour. r = red-haired n = non-red-haired b = beard or moustache red, scalp hair not red.
			400 mμ	530 mμ	650 mμ		
18-1	m.	36	2·2	2·6	3·5	60	b
2	f.	43	2·8	4·6	7·4	53	n
3	m.	11	3·0	4·9	9·5	44	
4	f.	5	2·2	3·2	5·2	52	
19-1	m.	—	—	—	—	—	r
2	f.	50	2·6	3·1	4·0	63	n
3	m.	27	2·4	2·9	4·1	56	
4	f.	25	2·2	3·5	6·5	46	
5	f.	23	2·4	4·3	9·0	41	
6	f.	21	3·6	6·5	10·9	51	
7	f.	19	2·1	3·2	5·9	46	
8	f.	17	2·4	4·0	6·6	52	
9	f.	15	2·0	3·0	5·3	47	
20-1	m.	—	—	—	—	—	n
2	f.	43	3·2	4·7	7·4	53	n
3	f.	21	3·0	8·1	20·8	36	
4	m.	18	2·7	3·5	5·0	56	
5	m.	16	2·8	3·9	5·6	57	
6	m.	11	3·8	7·0	11·6	53	
21-1	m.	—	—	—	—	—	n
2	f.	—	—	—	—	—	n
3	f.	10	3·1	7·0	18·3	34	
4	f.	7	3·3	5·6	9·6	50	
5	m.	6	3·3	8·1	18·3	40	
6	f.	6	2·9	7·0	15·7	40	
22-1	m.	48	2·0	2·6	3·9	54	b
2	f.	—	—	—	—	—	n
3	f.	11	7·0	13·2	20·6	56	
4	m.	8	3·0	6·6	16·3	36	
23-1	m.	—	—	—	—	—	n
2	f.	37	3·1	5·9	10·4	49	n
3	m.	19	3·4	6·0	10·8	48	
4	m.	16	2·6	5·2	11·8	39	
24-1	m.	—	—	—	—	—	n
2	f.	—	—	—	—	—	n
3	m.	29	3·0	4·5	6·9	55	
4	f.	25	2·5	5·0	10·1	44	
5	m.	16	4·4	7·3	11·3	55	
25-1	m.	—	—	—	—	—	b
2	f.	33	4·9	9·9	16·7	52	r
3	f.	10	3·1	6·1	12·0	44	
4	f.	8	3·4	8·5	18·7	41	
5	m.	6	5·3	11·4	20·9	48	
26-1	m.	—	—	—	—	—	r
2	f.	—	—	—	—	—	n
3	f.	20	2·2	4·5	11·0	36	
4	f.	11	3·7	5·9	9·5	53	
27-1	m.	41	3·4	6·5	11·6	49	r
2	f.	36	2·7	4·9	11·2	37	r
*2E	f.	29	2·2	4·8	13·6	32	
3	m.	8	3·1	7·1	19·0	33	
4	f.	1	3·6	9·6	22·5	39	

* T = identical twin of preceding person, not used in calculation. E = earlier specimen of preceding person, not used in calculation.
† To the nearest year.

Specimen number (grouped by family) ·1 = father ·2 = mother ·3 etc. = children	Sex	Age†	Reflectance % at			R	Parents' former hair colour. r = red-haired n = non-red-haired b = beard or moustache red, scalp hair not red.
			400 mμ	530 mμ	650 mμ		
28-1	m.	53	7·1	11·9	17·7	58	n
2	f.	48	3·5	5·1	8·9	48	r
3	f.	22	2·6	3·0	4·5	53	
4	f.	19	4·3	8·0	16·7	42	
5	m.	12	5·5	10·3	18·7	48	
29-1	m.	40	2·4	2·9	3·7	62	n
2	f.	39	3·0	6·0	11·3	47	?r
3	m.	13	3·3	6·7	17·2	34	
4	f.	11	3·1	5·8	11·4	44	
30-1	m.	41	3·5	4·6	6·8	56	n
2	f.	42	3·5	7·0	14·0	44	r
3	m.	12	3·8	7·0	14·7	41	
4	f.	9	4·9	10·4	19·1	48	
31-1	m.	43	2·2	2·3	2·8	64	b
2	f.	36	2·2	2·3	3·0	60	n
3	m.	6	2·5	3·1	4·4	57	
4	f.	4	2·2	4·1	11·1	32	
32-1	m.	43	3·3	4·5	6·7	55	b
2	f.	40	3·0	3·5	4·8	58	n
3	f.	14	3·0	6·0	15·2	35	
4	m.	4	5·0	8·9	14·1	55	
33-1	m.	—	—	—	—	—	n
2	f.	—	—	—	—	—	n
3	m.	19	2·9	5·1	13·0	34	
4	m.	18	2·4	3·5	6·4	45	
5	m.	12	2·2	2·6	3·6	58	
6	f.	10	2·7	4·4	7·7	48	
34-1	m.	—	—	—	—	—	n
2	f.	59	2·5	3·0	4·6	52	?
3	m.	28	2·4	2·5	3·1	61	
4	m.	26	3·9	8·6	15·6	49	
5	f.	24	2·5	4·5	14·3	27	
35-1	m.	—	—	—	—	—	n
2	f.	38	2·6	3·5	5·2	56	n
3	m.	13	2·8	5·6	14·0	35	
4	m.	4	3·2	7·3	17·4	37	
36-1	m.	—	—	—	—	—	n
2	f.	60	3·0	5·1	9·5	46	r
3	m.	33	2·3	2·8	4·0	55	
4	f.	28	2·6	5·5	14·3	34	
37-1	m.	—	—	—	—	—	n
2	f.	47	3·3	4·2	6·4	53	n
3	m.	12	4·0	6·4	10·3	52	
4	f.	6	2·1	5·3	16·5	29	
5	f.	6	2·5	6·0	17·1	32	
38-1	m.	—	—	—	—	—	r
2	f.	36	2·5	3·4	5·9	47	r
3	m.	10	2·4	3·9	8·0	41	
4	m.	4	2·6	5·5	14·8	33	
39-1	m.	—	—	—	—	—	r
2	f.	—	—	—	—	—	n
3	m.	22	3·5	5·6	9·4	51	
4	m.	16	2·7	5·7	14·3	35	

* T = identical twin of preceding person, not used in calculation. E = earlier specimen of preceding person, not used in calculation.   † To the nearest year.

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