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HEREDITY OF HAIR COLOR IN MAN

GERTRUDE C. DAVENPORT and CHARLES B. DAVENPORT

Station for Experimental Evolution, Carnegie Institution of Washington

Introduction

Types of Hair Color.—The heredity of hair color in mammals is a subject of great complexity, not to be lightly entered upon. It is a subject in which much knowledge has been gained in recent years through the work of Bateson and his associates, Castle and his pupils, Cuenot and others. Nevertheless certain important points remain uncertain. First, and fundamental for our purpose, is the question of the number of factors involved in any hair color. All are agreed that there is a special red pigment (a lipochrome) that stains the hair diffusely. In clear red hair one sees, in sections, a yellowish red tinge that is not bound up with any structures. With a high power one sees elongated, spindle-shaped bodies, which are apparently the remains of nuclei and are devoid of granules. In all other hair (except that of albinos) one sees granules grouped in the spindle-shaped bodies. In black hair (Chinaman, Fig. A) these granules are large and numerous in each group (average, 12) and appear of a dark brown color. In very dark brown hair (negro, Fig. B) the granules are perhaps a little larger but much less numerous in each group (average, 6); and the color is a much less intense brown. In hair of a cold, mouse brown (Fig. C) (about No. 25 in

E. Fischers's hair scale[1]) the granules are small, very few in each group (average 4) and slightly colored. The dark red hair of the orangutan is due chiefly to granules whose color is well reproduced by sepia on a clear background; but in the head hair of the golden babboon, which is striped golden and black, much diffuse golden pigment is found and (in the black zones) dark sepia granules of

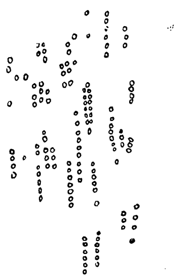

FIG. A. × 1150. CHINAMAN.

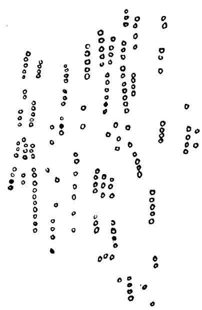

FIG. B. × 1150. LEON M. (NEGRO).

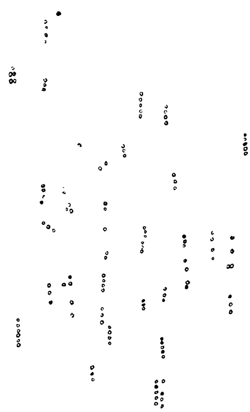

FIG. C. × 1150. MOUSE-BROWN. "A."

medium size and frequency. In twoscore preparations of the hair of man and primates we have not found in any instance jet-black granules such as are characteristic of black mice. In our preparations, many of which are thin sections kindly cut for us by Miss Lutz, the granules vary in size, number and intensity, but there is no discontinuity between the lighter and darker sepia pigments; and, as stated, we have not found a coal black hair either in Chinese, Japanese, Indian, Negro or Italian, and not even in the black spider monkey. There is an interesting parallel case in poultry where even in the Black Minorcas and the Black Cochin the pigment is a dense sepia brown. We conclude, therefore, that such discontinuous color types as are described in domesticated animals such as

[1] Made by Franz Rosset, Freiburg i/Br. See E. Fischer, *Korrespondenz. Blatt, Deutsch. Gesell. f. Anthropologie, Ethnologie u. Urgeschichte,* XXXVIII, 141–147. September–December, 1907.

fancy mice and guinea pigs under the names of yellow, chocolate and black are not fundamentally distinct, but have probably been made so in the process of perfecting the standard groups. Indeed, a casual acquaintance with the variety of human hair color as one meets with it in the streets of any large city shows that there are all intergrades between yellow, light brown, dark brown and black hair and even the reds pass (through dark red and red brown) into the warm browns. It may consequently be concluded, at least provisionally, that there are two main types of pigment in human hair; a reddish yellow, which finds its intensest development in bright red, and a sepia brown whose intensity varies from a light yellow to dark brown and black. Finally, the two pigments may be combined[2] and in such cases the brown pigment may quite obscure the red.

The conclusion here reached concerning the factors involved in human hair color are not, we fear, in accord with the recent investigations on other mammals. They rather speak against the theory of well-developed unit characters in human hair pigment. Brown and black colors there are and an intensifier or a diluter; on the other hand, these are not well defined units but occur in all conceivable degrees. The facts of intensity in human hair color indicate that the absence of selection made on the basis of intensity has resulted in the blending of color unit characters or has not afforded the selective means by which they have elsewhere been formed.

General Scheme of the Tables.—The data concerning a single family are placed in one line. At the extreme left are given certain reference letters by which the family is designated. Then follow the number of children in the designated family that have hair of the class named at the top of each column. The following six columns give the color of the hair of the mother (M), father (F), mother's mother (MM), mother's father (MF), father's mother (FM) and father's father (FF) so far as known.

[2] It is clearly seen in the hair of the mother of the *Lyn* family (Table X, *b*).

The principal abbreviations of the names of hair colors are as follows: *br*, brown; *chest*, chestnut; *dk*, dark; *fl* or *flax*, flaxen; *gold*, golden; *lt*, light; *med*, medium; *n*, black; *v*, very; *yell*, yellow. Names of colors in parentheses ( ) indicate juvenile condition.

Classification of the Tables.—Three series of tables may be considered. A, including cases where black or brown pigment is absent from both parents; B, including cases when brown is present in both parents and red is not visible in either; and C, including cases where both brown and red are visible in the parentage.

A. HEREDITY IN ABSENCE OF BLACK OR BROWN PIGMENT IN PARENTAGE

TABLE I. DISTRIBUTION OF HAIR COLOR IN OFFSPRING WHEN NEITHER PARENT SHOWS BROWN PIGMENT

Reference Letters.	Offspring. Tow.	Yell.	Gold.	Red.	Ancestry. M.	F.	MM.	MF.	FM.	FF.
Rit	4				flax	flax	flax	flax	flax	flax
Hak	11	2			lt. yell.	flax	"lt."	"lt."	"lt."	flax
Dex	1	4			blond	blond	blond	blond	blond	blond
Ste-E	2				gold	flax	br.	br.	lt. br.	N(flax)
Reg-A			6		gold	gold	gold	gold	gold	gold
Edw				3	dk. red	lt. red	—	—	—	—
Swe	2		1		lt. red	flax	lt. br.	dk. br.	dk. br.	dk. br.

B. HEREDITY OF BLACK AND BROWN PIGMENT IN PARENTAGE

TABLE II. DISTRIBUTION OF HAIR COLOR IN OFFSPRING OF PARENTS ONE OF WHOM HAS THE LEAST INTENSITY OF BROWN (FLAXEN, GOLDEN) AND THE OTHER A SLIGHTLY GREATER INTENSITY OF BROWN (LT. BR.)

Reference Letters.	Offspring. Flax.	Yell.	Yell.-Br.	Lt. Br.	Red.	Ancestry. M.	F.	MM.	MF.	FM.	FF.
Boy-A	2					flax	lt. br.	lt. br.	blond	lt. br.	lt. br.
Hal-A		1		2	1	lt. br.	flax	N.	lt. br.	flax	flax
Deg			1	1		lt. yell.	lt. br.	br.	dk. br.	lt. br.	lt. br.

The foregoing 7 families, comprising 36 children, illustrate a simple case. When both parents lack the brown pigment the children will all lack it. When the diffuse pigment has a weak intensity in the parents it will have the same character in the children; but where it has a strong intensity, as red, in the parents it may have the strong intensity in some (Swe) or all (Edw) of the children.

As compared with Table I, Table II shows a greater variation in the offspring—the classes light brown and yellow brown make their appearance and comprise just 50 per cent. of the offspring, a result that accords with the hypothesis that light brown is heterozygous and flaxen or light yellow is recessive, for, DR × RR is expected to yield 50 per cent. of the DR (light brown) type. We note here as in Table I that the hair is in no case darker in the children than in the darker parent; but it may be less dark.

TABLE III. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN BOTH PARENTS HAVE LIGHT BROWN HAIR

Reference Letters.	Offspring.					Ancestry.					
	Flax.	Gold.	Yell.-Br.	Lt. Br.	Auburn.	M.	F.	MM.	MF.	FM.	FF.
Byr		3	1		2?	lt. br.	lt. br.	dk. br.	N.	lt. br.	br.
Klo	2	1		1		lt. br. (fl.)	lt. br. (fl.)	lt. br. (fl.)	N.	"lt."	br.
Pla-B				6		lt. br.	lt. br.	lt. br.	lt. br.	N.	N.
Ste-G				2		lt. br.	lt. br.	br.	lt. br.	br.	—
Tuc				2		lt. br.	lt. br.	lt. br.	N.	dk. br.	gold
Totals	2	4	1	11	2?						

Assuming two cases of "auburn brown" in Byr family to be essentially golden brown (this hair has not been seen by us) it appears that when both parents have light brown hair either all of the children are of the same type (Pla-B, Ste-G, Tuc. families) or else of the light brown and lighter (yellow brown to flaxen—Byr?, Klo. family). In the first case the parents act like homozygous dominants toward the lighter types; in the second case like heterozygous dominants.

In this case we obtain a total of 42 offspring, 16, or 38 per cent., dark brown and brown, and 26, or 62 per cent., light brown or lighter. Taking dark brown as hetero-

Table IV. Distribution of Hair Color in the Offspring when One Parent has Dark Brown Hair and the Other Light Brown

(*a*) *The Darker Parent Produces "Light" Germ Cells as well as "Dark."*

Reference Letters.	Offspring.								Ancestry.					
	Flax.	Yell.	Yell.-Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	M.	F.	MM.	MF.	FM.	FF.
Bri					4		1		dk.br.	lt.br.	lt.br.	dk.br.	dk. br.	flax
Dou-A				1	2	2	1	1	dk.br.	lt.br.	lt.br.	dk.br.	dk. br.	lt. br.
Dou-B			1				3		lt.br.	dk.br.	dk.br.	lt.yell.br.	dk.red	N.
Fir		1			3				lt.br.	dk.br.	br.	br.	br.	dk.br.
Loc-B			2						dk.br.	lt.br.	yell.-br.	dk.br.	lt.br.	yell.-br.
Loe					4				dk.br.	lt.br.	lt.br.	N.	dk.br.	dk.br.
Mat-B					2				lt.br.	dk.br.	br.	dk.br.	lt.br.	dk.br.
Mor-A					2				dk.br.	lt.br.	lt.br.	dk.br.	dk.br.	N.
Ran-B					3	3	3		dk.br.	lt.br.	lt.br.	br.	br.	lt.br.
Sho					1		2		dk.br.	lt.br.	lt.br.	lt.red	dk.br.	br.
Totals		1	3	1	21	5	10	1						
		26				16								

zygous and dominant to light, expectation is 50 per cent. of the offspring as dark as or somewhat less dark than the darker parent and 50 per cent. light. The observed frequencies are of the expected order.

(*b*) *The Darker Parent is not Known to be Heterozygous in Hair Pigment.*

Reference Letters.	Offspring.					Ancestry.					
	Flax.	Gold.	Lt. Br.	Br.	Dk. Br.	M.	F.	MM.	MF.	FM.	FF.
Bin			1	2		dk. br.	lt. br.	dk.br.	N.	br.	dk. br.
Fis			3		1	dk. br.	lt. br.	dk.br.	dk.br.	lt. br.	lt. br.
Fri			2		1	dk. br.	lt. br.	br.	N.	br.	blond
Gil-B	1		2		1	dk. br.	lt. br.	dk.br.	dk.br.	lt. br.	lt. br.
Gue	2			2	1	lt. br.	dk.br.	dk.br.	N.	dk. br.	N.
Hal-E			1	2	2	dk. br.	lt. br.	br.	br.	N.	lt. br.
Huf	1		2			lt. br.	dr. br.	lt. br.	dk. br.	dk. br.	dk. br.
Lat-A		2	2		1	v. dk. br.	lt. br.	N.	N.	N.	N.
Pot			2		2	dk. br.	lt. br.	dk. br.	dr. br.	dk. br.	dk. br.
Rog-B			3		1	dk. br.	lt. br.	dk. br.	dk. br.	N.	lt. br.
Sin					2	lt. br.	dk.br.	lt. br.	—	"dark"	dk. br.
Sne			2			lt. br.	dk.br.	lt. br.	dk. br.	dk. br.	N.
Wil-D		1	1	2	2	lt. br.	dk.br.	lt. br.	lt. br.	dk. br.	N.
Totals	4	3	21	8	14						
		28		22							

In this case we obtain in a total of 50 offspring, 22, or 44 per cent., dark brown and brown and 28, or 56 per cent., light brown or lighter. Were the dark brown parents truly homozygous in hair color, and did the hair color of the offspring not grow darker with age, Mendelian expectation would be 100 per cent. dark brown. Actually, the result falls far short of that, just as the necessary conditions are far from being met. It is highly probable that in some of these families (notably Gil-B, Gue and Huf, and probably also Lat-A and Wil-D) the darker parent actually forms germ cells that lack black pigment. Of the four lightest haired children the ages of three that are known are 8, 10 and 15 years—ages at which the adult color is not fully shown. Under these circumstances one can not predict with certainty the outcome of matings of this class. One can only say that the proportions of light brown children and those with lighter hair should be less in proportion to the darker haired children in class B than in class A. The actual proportions in the two classes are in the direction of this expectation.

TABLE V. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN ONE PARENT HAS BLACK HAIR AND THE OTHER LIGHT BROWN HAIR (NO DIVISION, ON ACCOUNT OF FEWNESS OF FAMILIES)

Reference Letters.	Offspring.							Ancestry.					
	Flax.	Yell. Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	M.	F.	MM.	MF.	FM.	FF.
Car-B				1	3		1	N.	lt. br.	br.	N.	lt. br.	lt. br.
Dey				3				N.	lt. br.	dk. br.	N.	br.	N.
Dra		1		1				N.	lt. br.	dk. br.	N.	dk. br.	dk. br.
Jem				2		1		N.	lt. br.	lt. br.	N.	dk. br.	lt. br.
Ski		1		2		2		lt. br.	N.	"fair"	br.	N.	N.
Ser						2		N.	lt. br.	dk. br.	"light"	lt. br.	N.
Spr			1	1	1	1		lt. br.	N.	—	—	—	—
Str-B	2	1		3				lt. br.	N.	N.	lt. br.	lt. br.	—
Tre				2	1			N.	lt. br.	N.	dk. br.	—	—
Totals	2	3	1	15	5	6	1						
	21				12								

Assuming what is probably true for all the families, that the black-haired parent produces an equal number of germ cells with a tendency toward lighter hair and toward black, we should expect an approach toward an equality of light and dark haired offspring. Actually, the lighter colors are in excess—a result again doubtless due to the

TABLE VI. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN ONE PARENT HAS BLACK HAIR AND THE OTHER BROWN HAIR

Reference Letters.	Offspring.						Ancestry.					
	Flax.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	M.	F.	MM.	MF.	FM.	FF.
Blo-A			3	2			N.	br.	—	—	—	—
Cas		1	1				N.	br.	br.	N.	flax	N.
Clu-A				3			br.	N.	—	—	—	—
Clu-B			1	1		1	br.	N.	—	—	—	—
Col-C	1		1	2	1		br.	N.	lt. br.	N.	dk. br.	lt. br.
Dru-B			3				N.	br.	—	—	—	—
Hen			1	1	1		br.	N.	N.	br.	N.	yell.-br.
Hof		1	2				br.	N.	lt. br.	lt. br.	N.	N.
Koo		1	[illegible]	1			br.	N.	br.	br.	br.	br.
Lea			1	2			br.	N.	br.	br.	br.	br.
Mil-A			1	1	1		N.	br.	br.	N.	N.	br.
Ros			3	2			N.	br.	br.	br.	br.	N.
Sea				4			br.	N.	br.	br.	br.	N.
Ste-D						7	br.	N.	N.	—	—	—
Sto-B					1	1	br.	N.	br.	dk. br.	br.	N.
Ver		1			1		N.	br.	br.	lt. br.	dk. br.	N.
Totals	1	4	17	19	5	9						
		22			33							

relative immaturity of the children as compared with their parents.

Assuming, as in the discussion of Table V, that the blacks are heterozygous (except in the Ste-D family) we should expect an equality of dark and light haired offspring modified by preponderance of the lighter type owing to the immaturity of the average of the offspring. Actually, with brown hair and lighter there are 41 children as opposed to 7 (Ste-D omitted) kith either black or dark brown hair. When we compare the proportion of the children having hair brown or darker in this Table (60 per cent.), with that in Table V (36 per cent.) we realize how much more frequent the darker classes have become with the increased darkness in the hair of the second parent.

On account of the impossibility of drawing the line between the dark and the light shades of hair and on account of the light color of immature offspring we are able only to compare this section with that which follows.

TABLE VII. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN BOTH PARENTS HAVE DARK BROWN OR BLACK HAIR

(a) When Both Parents Probably Form Light Germ Cells and Dark in Equal Numbers

Reference Letters.	Offspring.								Ancestry.					
	Yell.	Yell.-Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	Chest.-Br.	M.	F.	MM.	MF.	FM.	FF.
Cam-A	1			4	3		2		N.	N.	"med."	N.	lt.br.	N.
Can				2					N.	N.	dk.br.	N.	dk.br.	lt.br.
Cla-A				1		3			dk.br.	dk.br.	lt.br.	dk.br.	lt.br.	lt.br.
Cur				1		1			dk.br.	dk.br.	lt.br.	br.	lt.br.	dk.br.
Fue	1	1				1			dk.br.	dk.br.	blond	dk.br.	dk.br.	blond
Gla-B	1	1		2		2	1		N.	N.	yell.-br.	N.	N.	br.
Gor-A			2	3		2	4		dk.br.	N.	N.	br.	N.	br.
Had				2	1				dk.br.	N.	N.	lt.br.	br.	N.
Har-A		1		3		3	2		dk.br.	N.	br.	br.	br.	br.
Hem-A				1	1	1			br.	N.	N.	br.	N.	yell.-br.
Mck						1		1	N.	N.	br.	br.	N.	br.
Rol				1		4	1		N.	dk.br.	br.	N.	lt.br.	dk.br.
Sim			1			1			N.	N.	N.	lt.br.	lt.br.	lt.br.
Totals	3	3	3	20	5	19	10	1						
	29				35									

Assuming that the qualities of light hair color and dark hair color (or absence and presence of intensifier) segregate in parents of mixed origin expectation is that Series A would yield 75 per cent. dark haired offspring, but on account of the impossibility of drawing the line between the dark and light shades of hair and on account of the light color of immature offspring we are able only to compare this series with series *b* in which expectation is 100 per cent. offspring of the darker color. Actually, in series *b* there are 59 individuals light to 137 (or about 70 per cent.) dark while in series *a* only 55 per cent. are dark. A part of these light haired individuals probably result from recessive light hair color of parents and a part from immaturity.

(b) When Both Parents are not Known to Form Light Germ Cells

Reference Letters.	Offspring. Flax.	Yell.	Yell.-Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	Chest.	Red.	Ancestry. M.	F.	MM.	MF.	FM.	FF.
Bal					3		3				dk.br.	dk.br.	dk.br.	dk.br.	dk.br.	N.
Bar-A					4		2				dk.br.	dk.br.	N.	N.	dk.br.	N.
Bec-A					1	1	1	1			dk.br.	N.	lt.br.	N.	N.	N.
Bra-C					1		1				dk.br.	dk.br.	N.	lt.br.	—	dk.br.
Bra-D						1	3	2			N.	N.	dk.br.	N.	N.	dk.br.
But			1				2	1			dk.br.	N.	N.	N.	N.	dk.br.
Can					2						N.	N.	dk.br.	N.	dk.br.	lt.br.
Cap					1		3				N.	N.	N.	N.	N.	—
Cla-C							2				N.	dk.br.	br.	N.	lt.br.	lt.br.
Cla-D					2		3				dk.br.	dk.br.	br.	dk.br.	br.	dk.br.
Dav-B					2	1	1				dk.br.	N.	N.	N.	N.	N.
Dor-B					2		2	3			N.	N.	br.	N.	N.	N.
Fal				1	2	1	2	1			dk.br.	dk.br.	N.	N.	N.	yell.-br.
Fie	2				1	1	1				dk.br.	N.	br.	dk.br.	dk.br.	br.
Gar		[1][1]			[1][2]			3			N.	N.	N.	N.	N.	N.
Gra-A		1			1	1	1				dk.br.	dk.br.	N.	N.	yell.-br.	N.
Gre-A							2				N.	dk.br.	N.	N.	dk.br.	dk.br.
Gro-A						1	2				dk.br	dk.br.	dk.br.	dk.br.	dk.br.	dk.br.
Hed					1	2	1	1			dk.br.	dk.br.	br.	N.	N.	br.
Hew-A					1[3]		2	2			N.	N.	N.	N.	N.	N.
Hit					1		1				dk.br.	N.	N.	N.	dk.br.	dk.br.
How-B	1				3		2				dk.br.	N.	dk.br.	N.	—	N.
Keh							4	1			N.	N.	N.	N.	N.	N.
Lay					3	2					dk.br.	dk.br.	br.	br.	dk.br.	dk.br.
Leo					1	1	1				N.	dk.br.	gold	N.	N.	dk.br.
Lit-B					1	2					dk.br.	dk.br.	dk.br.	dk.br.	br.	lt.br.
Los					1		2	1			N.	N.	N.	N.	br.	yell.-br.
Mag					2		4				dk.br.	N.	dk.br.	N.	N.	dk.br.
Meb						1	3	1			N.	N.	—	—	N.	—
Nor	3						3				dk.br.	dk.br.	dk.br.	N.	N.	flax
Oke					1	1		1	1		dk.br.	N.	br.	N.	N.	N.
Par-B						1	2				N.	dk.br.	br.	N.	N.	N.
Poe			1			2					dk.br.	N.	N.	yell.-br.	N.	N.
Put					2		4				dk.br.	dk.br.	dk.br.	dk.br.	lt.br.	N.
Ram						1		1		1	N.	N.	N.	N.	N.	N.
Rem	1					1					dk.br.	dk.br.	dk.br.	dk.br.	dk.br.	dk.br.
Ric-C					1		1	1		2	N.	N.	N.	N.	N.	N.
Rob-B						2	1	2			N.	dk.br.	br.	N.	br.	dk.br.
Sam-B			2		1		2				dk.br.	dk.br.	N.	N.	N.	N.
Sel					1		1	2			dk.br.	N.	dk.br.	N.	N.	N.
Squ					1		1	3			N.	N.	N.	N.	N.	N.
Sto-C							2				N.	N.	N.	N.	dk.br.	N.
Tho-D					1	1		1			dk.br.	N.	dk.br.	N.	dk.br.	N.
Tru	1						2				dk.br.	dk.br.	dk.br.	yell.-br.	dk.br.	dk.br.
Was						1	2	2			dk.br.	dk.br.	N.	N.	dk.br.	dk.br.
Whe-A						5		1			N.	N.	N.	dk.br.	—	—
Wol		1[4]									N.	N.	N.	N.	N.	N.
Totals	8	2	4	1	44	30	72	31	1	3						
	59					137										

[1] 9 years old. [2] 6 years old. [3] Also 3 flaxen, 5 to 10 years old. [4] Also 3 "blond," 1–9 years old.

C. Heredity of Red and Brown Pigment

We have seen that the red series is quite independent of the yellow-brown series. Clear red-haired individuals lack black pigment themselves and can not transmit it to their offspring. This is, at least, *a priori* probable; but despite careful search we have found no case of two parents with clear red hair. One case of clear red and dark red is given in Table I., Edw family, in which all three children have red hair. We have one of dark red × dark red parentage with the following remarkable record (as yet unchecked).

Reference Letters.	Offspring.				Ancestry.					
	Yell.	Gold.	Brown.	Black.	M.	F.	MM.	MF.	FM.	FF.
Dey-B	1	3	1	4	dk. red	dk. red.	—	N	br.	N

We interpret this case to mean that the red is absent in some children (owing to heterozygotism of the parents) and dilute in others and here masked by black pigment.

Table VIII. Distribution of Hair Color in the Offspring when One Parent has Hair of a Clear Red Color; the Other of a Brown

Reference Letters.	Offspring.								Ancestry.					
	Flax.	Yell. Br.	Lt. Br.	Br.	Dk. Br.	N.	Chest.	Lt. Red	M.	F.	MM.	MF.	FM.	FF.
Bon								4	br.	lt. red	N.	br.	br.	br.
Bow		1	2		1		1		red	br.	N.	N.	—	br.
Dig			4			1			N.	red	—	—	—	—
Hur	1		3						lt. red	lt. br.	lt. br.	dk. br.	lt. br.	dk. br.
May	[1]		1				1		lt. red	br.	lt. red	flax	yell. br.	dk. br.
Web		1	1	1		2		2	lt. red	N.	lt. red	N.	N.	N.
Totals	1	2	11	1	1	3	2	6						

In this table the yellow-brown series of colors predominates among the offspring over the reds. This we interpret to mean that, as the red parents are usually heterozygous in the intensity of red that they bear, we have approximately one half of the offspring without any (or only a slight) tendency toward red. Even when red dominates over its absence it is frequently completely hidden by black or even dark brown. In consequence of the cooperation of these two causes we are not surprised to find considerably more than half of the offspring (70 per cent.) *showing* no red.

TABLE IX. DISTRIBUTION OF HAIR COLOR IN THE OFFSPRING WHEN THE PARENTS HAVE DARK HAIR CONTAINING HYPOSTATIC RED.

(*a*) *Both Parents Have Hypostatic Red*

Reference Letters.	Offspring.										Ancestry.					
	Flax.	Yell.	Yell. Br.	Gold.	Lt. Br.	Br.	Dr. Br.	N	Chest.	Lt. Red.	M.	F.	MM.	MF.	FM.	FF.
Ear						1				1	dk.br.	dk.br.	dk.br.	lt. red	dk.br.	red
Hog-B					1		1		1		dk.br.	dk.br.	chest.	N.	chest.	—
Kel					1					2	N.	N.	—	—	—	—
Smi-D							1		3		dk.br.	N.	N.	chest.	chest.	chest.
Totals					2	1	2	0	4	3						

(*b*) *Only One Parent is Known to Have Hypostatic Red.*

Reference Letters.	Flax.	Yell.	Yell. Br.	Gold.	Lt. Br.	Br.	Dr. Br.	N	Chest.	Lt. Red.	M.	F.	MM.	MF.	FM.	FF.
Beo-A					2	1	2	5			N.	N.	br.	chest.	br.	N.
Dev					1		1				dk.br.	N.	lt.br.	N.	—	red
Gla-A						3	3	2			N.	dk.br.	N.	chest.	dk.br.	N.
Got		1		1			1	1			N.	N.	N.	N.	N.	red
Pat-A			1		1	4	3	1			N.	N.	red	dk.br.	N.	N.
Wan-A					1	1	1				N.	dk.br.	dk.br.	dk. red	br.	dk.br.
Wel-A	2					2	5	1			N.	dk.br.	N.	dk. red	—	dk.br.
Whe-D						1		1			N.	N.	dk. red	N.	lt.br.	N.
Woo-B							2				N.	dk.br.	dk.br.	gold	chest.	gold
Totals	2	1	1	1	5	12	18	11								

Tables VIII to X give data for answering the very difficult question of inheritance of red when associated with melanic pigment. The chief difficulty is due to the masking of the diffuse by the more intense granular pigment. The following results seem, despite this difficulty, established.

1. Two light-haired parents whose hair is without red will have no red-haired children (Table I).

2. When one parent only forms "red hair" gametes, while the other forms exclusively gametes containing the darker phases of melanic pigmentation, the offspring will show no red hair; *a fortiori,* if neither parent forms "red hair" gametes, no red hair will appear in the offspring. (Table IX, *b*; compare also Tables IV, V, VI and VII.)

TABLE X. DISTRIBUTION OF HAIR COLOR IN FAMILIES CONTAINING RED-HAIRED CHILDREN; AND THE HAIR COLOR OF THE ANCESTORS OF THESE FAMILIES

Reference Letters.	OFFSPRING.											ANCESTRY.					
	Flax.	Yell.	Yell.-Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	Chest.	Lt. Red.	Dk. Red.	M.	F.	MM.	MF.	FM.	FF.
(a) Both Parents Have Red Visible in Hair																	
Edw										2	1	dk.red	lt.red	—	—	—	—
(b) Only One Parent Has Red Visible in Hair																	
Bur-B						3				1		auburn	dk.br.	auburn	auburn	dk.br.	dk.br.
Bow										4		br.	br.-red	N.	br.	br.	br.
Fin				1						1		dk.br.	dk.red	dk.br.	dk.br.	lt.br.	dk.br.
Hol-D							1			1		red	dk.br.	dk.br.	br.	N.	br.
Lyn				2						1	1	red.-br.	br.	chest.	br.	br.	br.
Mur			1		1						1	dk.red	lt.br.	dk.red	N.	dk.br.	dk.br.
Mye					1	1				2		br.	dk.red	red	br.	N.	br.
Pad					1						4	lt.br.	dk.red	N.	N.	—	—
Rav					1					1		dk.red	dk.br.	dk.red	—	—	—
Wri										3		dk.br.	sandy	dk.br.	br.	sandy	br.
Web			1		1	1		2		2		dk.red	N.	N.	br.-red	N.	N.
Totals			2	3	5	5	1	2	0	16	6						
					18					22							
(c) Neither Parent has Red Visible in Hair																	
Bol		1	1						1	1		yell.-br.	N.	lt.br.	dk.br.	—	—
Ear						1				1		dk.br.	dk.br.	v.dk.br.	br.-red	dk.br.	red
Elt					2					1		br.	lt.br.	dk.br.	lt.br.	lt.br.	br.
Fan						1		2		2		br.	N.	N.	N.	N.	N.
Fra-D											2	N.	N.	—	—	—	—
Fri-B					2	2					1?	lt.br.	lt.br.	br.	lt.br.	lt.br.	—
Fro					1	1	1			1		lt.br.	br.	br.	lt.br.	—	—
Gri			1		1		2	1	1		1	N.	br.	yell.	dk.br.	red	N.
Had-A											2	N.	br.	N.	N.	N.	br.
Kel					1					2		N.	N.	—	—	—	—
Mcg-B					1	3				3		N.	br.				
Pra		1		3		2	1			1		yell.-br.	dk br.	gold	N.	N.	dk.br.
Ram						1		1			1	N.	N.	N.	N.	N.	N.
Ric					1		1	1		2		N.	N.	N.	N.	N.	N.
Sco			2	1			1			1	1	lt.br.	N.	br.	N.	red	N.
Tay					1		1				1	lt.br.	dk.br.	br.	br.	br.	dk.br.
Wal-C						2	1			3	2	br.	N.	N.	dk.br.	dk.br.	N.
Wri-A					3		1	1		2		dk.br.	N.	dk.br.	N.	red	br.
Totals		1	4	5	13	13	9	6	2	20	11						
					51					33							

3. When, on the other hand, both parents, though very dark, produce "red hair" gametes, about three sixteenths of the offspring will have clear red hair. (Table IX, *a*; the ratio is 3 in 12.)

4. Conversely red-haired children result from the union of two "red hair" gametes. If there is no black pigment to be considered all children, in such cases, will have red hair. If one parent has visible red and the other none (though probably heterozygous) then about half of the children show the lipochrome pigment and the other half the melanic pigment (Table X, *b*). If neither parent of red-haired children shows red in its (dark) hair then expectation is that only three sixteenths of the offspring will have red hair. Table X, *c*, shows only those families in which red actually occurs. Now in some families with the potentiality of red in one quarter of the offspring, but having only four or fewer children, a red-haired child may fail to occur and such a family would be excluded from the table. Such an exclusion would tend to reduce the proportion of non-red offspring in the total. Consequently instead of 86 per cent. of the offspring in Table X, *c*, being non-red, actually only 61 per cent. are such. In the families given there are numerous cases where the red haired are to the non-red haired offspring as 3 is to 13 or as nearly so as the size of the family permits. This is true of the Bal, Elt, Fro, Gri, Ram, Sco and Tay families. The other families show not unreasonable divergencies from the typical 3 to 13.

5. All results are in accord with the statement that red and black constitute two independent series; that red is dominant over no red, as the deeper shades of melanic pigment are dominant over the lighter; and that the dense granular melanic pigment tends to hide the diffuse pigment. Thus in Table VIII the gametes of the red-haired parent may be given as n.R; those of the brown-haired parent as N.r; where N, n. are abundance and sparsity of melanic pigment, respectively, and R, r presence and absence of lipochrome (red) pigment, respectively. Then the zygotes will be of the various forms: nR (red soma), NR (brown or black, red hypostatic), Nr (plain brown or black), n.r. (flaxen to light brown). The matings of Table IX, *a*, are of the order (NR, Nr, nR, nr) $\times$ (NR,

Nr, nR, nn). Expectation in 12 offspring is 6.7 dark brown or chestnut, 2.3 clear red, 2.3 pure brown or black and .7 very light brown. This expectation is approximately realized in the totals. The matings of Table IX, *b*, are of the order (NR, Nr, nR, nr) × (Nr). There is actually a total of 51 individuals and expectation in this case is 25.5 offspring with deep melanic or chestnut hair and 25.5 offspring with pure melanic pigmentation of some grade. No pure red should appear and none does occur. The matings of Table X, *b*, are of the order (NR, nR) × (nR). They should give an equality of offspring of the two types: NnRR (melanic pigmentation with hypostatic red) and nnRR (red with little or no black). The matings of Table X, *c*, are of the order (NR, nR, Nr, nr) × (NR, nR, Nr, nr). This should yield in a total of 73 offspring 43.9 having dark melanic pigment combined with (hypostatic) red; 14.6 with pure brown of some grade; 14.6 with pure red and 4.9 with sparse melanic pigmentation (yellow brown). The important proportional excess of the reds is explained in the last paragraph.

D. Is Inheritance of Hair Color at all Blending and can it be said to Conform to Galton's Law?

We have seen that, despite the difficulties offered by change of hair color with age and by the masking of diffuse red pigment with brown granular pigment, inheritance in hair color can be brought into accord with the ordinary formula for alternative inheritance. But it may fairly be asked, since brown pigment is not a well-defined unit character, whether hair color may not equally conform to the blending type of inheritance. If there were blending ("as in human skin color"?) then the offspring of a dark and light should all be intermediate. Table V is important in this inquiry. If blending occurred the offspring of black and light brown should all be brown (or light brown because of immaturity) but dark browns and a black occur; so in Table VI the 9 blacks oppose the hypothesis; also in Tables VIII and

IX, *a*, the occurrence of red is not in accord with the hypothesis. Certainly there is no blending in an "all N" ancestry of red and yellow as in the Ram, Ric-C and Wol families of Table VII, *b*. The results clearly do not accord with the law of blending inheritance.

It remains to consider if inheritance of hair color follows Galton's law which states that the two parents determine 50 per cent. of the ancestry, the four grandparents together 25 per cent. and earlier ancestry altogether form the remaining 25 per cent.

Taking the 12 families of Tables X, *c*, whose grandparents are all given, we have in the parentage a total of 0 red in 24 parents; and of 5 red in 48 grandparents, or about 10 per cent. Assuming the same proportion of red in the unknown earlier ancestry, we have the total expected proportion of red in the offspring given by the sum

$$\begin{aligned} 0 \div 24 \times 50 &= 0 \\ 5 \div 48 \times 25 &= 2.6 \\ .104 \times 25 &= 2.6 \\ \hline & \ \ 5.2 \text{ per cent.} \end{aligned}$$

Actually, there are about 40 per cent. of the red type, and, making every allowance, at least 18 per cent. are to be expected. Five per cent. certainly fits the facts very badly. We conclude, therefore, that Galton's law does not fit the facts as well as Mendel's law and that heredity of hair color is alternative.

E. The Non-transgressibility of the Upper Limit

While the application of the law of alternative inheritance to human hair color lacks something in ideal clearness and precision, one general rule stands out prominently. It is that in the midst of the varying degrees of intensity of the melanic pigmentation the intensity of the melanic pigmentation of the offspring never exceeds that of the more intense parent.

The general intensity relations of melanic hair pigment in parents and offspring are brought out in Table XI.

An inspection of this table shows that, in general, in

TABLE XI.

Grade of Darker Parent.	Hair Color of Offspring.								Red Series.
	Flax.	Yell.	Yell. Br.	Gold.	Lt. Br.	Br.	Dk. Br.	N.	
Flax	4								
Yell.	11	2							
Yell. br.	1	4							
Gold	2			6					
Lt. brown	4	1	2	5	14				3
Brown	11	4	4	4	23	24	5		
Dark brown	4	2	2	5	66	25	58	6	
Black	3	4	5	8	60	37	49	40	4

the melanic series, the grade of intensity of hair pigmentation in the offspring does not exceed that of the darker parent. The only exceptions appear in the "brown" and "dark brown" parentage, where a small percentage of children are represented as of the next darker grade. Many more such cases were in our original records, but wherever the question was asked of the recorder whether the hair of the child, *A*, exceeded in darkness that of the darker parent, *B*, the reply was almost without exception negative. Samples of hair were asked for and these never proved darker in the children than in the parents. A common source of error lies in not disconnecting the effect of a slight grayness in the parent. In one sample of hair from a mother that was reported lighter than the daughter the gray hairs were carefully picked out, when it appeared that the natural color of the hairs of the mother and child were as like as possible. Consequently one is justified in laying no stress on the 11 children out of 600 (less than 2 per cent.) in which the hair color was returned as darker than that of the parents—particularly as despite efforts these returns could not be confirmed. It follows, then, that parents may be assured that their children will eventually have hair as dark as the darker parent or of a lighter tint, but not darker. Consequently, parents with flaxen or yellow hair will have children all alike and like themselves in this respect. But parents with black hair may have children with flaxen hair or with light brown hair or (because of the masking qualities of black pigment) with red hair.

What is the relation of this principle to the law of alternative inheritance? The latter is only a special case of it. When characters A and B are crossed the more intense character appears in the offspring—the less intense character is recessive—the "heterozygous" children do not exceed the more intense parent. If, now, two such heterozygous persons be mated, one fourth of their offspring show the recessive condition, which by hypothesis is of a lower grade than that possessed by the parents; the remainder of the offspring may attain the grade of their parents; but they will not exceed that grade. This principle of the non-transgressibility of the upper alternative inheritance only, but also for blending inheritance—indeed, it seems to be of universal applicability.

An exception to this rule is exhibited by some heterozygous forms. The cross of a high-combed fowl and a low-combed is a fowl with one intermediate grade of comb. Two heterozygous combs in the parentage throw, *inter alia,* high combs. Not all cases of heterozygous forms constitute exceptions to this law of the non-transgressibility of the upper limit, and human hair color seems, even in the heterozygous condition, to follow the law. The workings of the principle are veiled in some cases of cryptomeric characters, *i. e.,* built up of hidden factors.

Certain important consequences flow from this principle. These one of us has pointed out in a brief communication to *Science.*[3] If the progeny stands on the average in respect to a character at a lower grade than the parents then, if inbreeding is practised, the two parents of the next generation will probably have this character at a lower level than their parents and will produce children having the character less well developed than they have it themselves. If inbreeding be practised for several generations it is clear that in some, at least,

[3] Vol. XXVIII. pp. 454–455, October 2, 1908.

of the children, the character in question would probably become quite degenerate. Since the note in *Science* was published we have read a paper by Feer, to which our attention was called by the title "Der Einfluss der Blutverwandschaft der Eltern auf die Kinder."[4] This paper comes very near to our point of view. After showing that retinitis pigmentosa and congenital deaf-dumbness are the diseases most closely associated with inbreeding the author concludes that they are not so much inheritable diseases in the usual sense as inheritable diseases of degeneration, and depend on degeneration of the embryonic ectoderm. It seems clear from such data as Feer adduces that our general thesis will hold true for many human characters—that inbreeding does not cause them to degenerate, but having a tendency to degenerate, inbreeding will prevent any recovery and, in addition, will hasten the downward tendency from generation to generation. The only way to avoid progressive degeneration is to bring in (usually necessarily from outside) blood with the tendency to produce the characteristic in a well-developed condition.

Combining now the results of the three studies on eye color and hair color and form made by us,[5] it appears that two parents with clear blue eyes and yellow or flaxen straight hair can have children only of the same type, no matter what the grandparental characteristics were; that dark eyed and haired, curly-haired parents may have children like themselves but also of the less developed condition. In the latter case what the proportions of each type will be is, for a fairly large family, predictable by a study of the immediate ancestry.

CARNEGIE INSTITUTION OF WASHINGTON,
DEPARTMENT OF EXPERIMENTAL EVOLUTION,
COLD SPRING HARBOR, N. Y.,
December 1, 1908.

[4] Separate, Berlin, 1907; also "Jahrbuch für Kinderheilkunde," Bd. LXVI.

[5] G. C. and C. B. Davenport, "Heredity of Eye-Color in Man," *Science*, N. S., XXVI, pp. 589–592, November 1, 1907; "Heredity of Hair-Form in Man," AMERICAN NATURALIST, XLII, pp. 341–349, May, 1908.