THE INCIDENCE AND MENDELIAN TRANSMISSION OF MID-DIGITAL HAIR IN MAN*

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HAIR is present on the basal segments of all fingers of the human hand, and is absent from the terminal segments. Individuals vary, however, in the presence or absence of hair on the mid-digital segments of the four fingers exclusive of the thumb. Both the presence and absence of mid-digital hair are so well distributed in white populations that the trait would have wide usefulness in chromosomal linkage studies, and in any other studies requiring "normal" heritable traits, if the mode of transmission could be definitely established.

Danforth,[3] in a study of mid-digital hair in 80 family groups, and in other groups classified by sex, racial origin, etc., concluded that "what seems to be a phylogenetically progressive loss of hair is brought about through the action of one or more recessive genes, or of one primary recessive gene with several modifying factors that regulate the distribution of hair when it is present" (p. 199). He also showed that the trait has anthropological significance.

In studies conducted by our laboratory primarily to search for linkage relationships in human traits, the distribution of mid-digital hair has been recorded routinely. A hand magnifying glass has been used to detect the presence of hair follicles on fingers with no visible hair, and in the present study, fingers showing follicles but not hair, as well as those bearing hair, have been counted as affected. No linkages have yet been established between mid-digital hair and other traits, but sufficient data are now at hand to permit further analyses of the incidence of mid-digital hair by age, sex, and natio-racial origin, its distribution among four digits of the hand, and its transmission in families.

Four sets of data are available:

1. *M.F.S. data:* 30 two-generation families located in a field study of myopia. At least one offspring per family had been a clinic patient at the Manhattan Eye, Ear, and Throat Hospital. The data comprise 201 subjects, 85 males and 116 females. Collected by Burks and a field assistant.
2. *H.H.S. siblings:* 99 pairs of two siblings and seven sets of three siblings studied at Huntington High School, Long Island. These include 100 boys and 119 girls of high school age. Collected by Burks.
3. *H.H.S. families:* 13 two-generation families — parents and siblings of H.H.S. pupils. These families were selected for follow-up because of large sibships. The data comprise 90 subjects, 45 males and 45 females. Collected by Burks.
4. *Supplementary families:* 8 two-generation families from among the acquaintance of the writers, included in order to gain further light on problems of diagnosis. The 30 subjects included 15 males and 15 females. Collected by Burks and Bernstein.

Although an effort was made to ascertain whether all offspring of a family group were full siblings, it is quite possible that concealed adoptions or illegitimacy may have influenced the results to some degree.

Influence of Age and Sex on Incidence of Mid-digital Hair

Danforth,[3] studying sections of skin of foetal and adult material concluded "that the (mid-digital) hair may be definitely present or absent from a very early period of life of the individual" (p. 191). We do not have sufficient data from very young subjects to check upon this finding, although it is interesting to note that the three youngest individuals among our subjects, aged 1, 1½, and 2½ years respectfully had no visible mid-

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digital hair nor follicles, while two subjects of four years did have mid-digital hair. We have not included children younger than four in our subsequent calculations. It is quite possible, however, that hair might be visible on the fingers of young children and infants whose activity has not rubbed it off, and in fact one of us has observed it incidentally in an infant of 11 months.

With respect to sex incidence Danforth found that "in all cases of comparable groups from two sexes it is the female group that shows the higher percentage of cases without hair on the mid-digital region" (p. 196). In his group of several hundred American whites, 39 per cent of the males and 54 per cent of the females lacked mid-digital hair. Danforth suggested, however, that the difference may be due at least in part to the greater frequency in the female of very rudimentary hair which may not always be detected.

A sex comparison of our data revealed no significant difference in the percentage (69%) of female and (67%) of male students of the H.H.S. with mid-digital hair. The ages of the students range from 14 to 22 years, the great majority being 15 to 18 years of age. For the offspring generation (ages 4 to 39) of the M.F.S. and H.H.S. family groups, no significant sex difference was found in age groups under 18 years of age (see Table I). Moreover the incidence of mid-digital hair showed no marked age trend in the males, but dropped decidedly in the group of females over 21 years of age.

The data strongly suggest that Danforth's explanation of sex differences is a sound one, but that further, the difficulty in the diagnosis of the mid-digital hair condition in females is not obtrusive before maturity, especially in environments where the demands for manual work are not heavy. After maturity, however, diagnosis of either mid-digital hair or follicles becomes uncertain in women (and probably also in men, but to far less degree). In our group of supplementary families collected with special reference to factors influencing the diagnosis of mature females, it was found that several women who appeared to be asymmetrical at first examination proved to have follicles that would balance the symmetry when re-examined with a 12-diameter lens. There were also cases with a few pits in the skin which we could not be sure were follicles.

Natio-racial Variation

Danforth reported that "the Indian, the Negro, and the Japanese, as races, have gone farther toward freeing the mid-digital region of hair than has the white race, although certain members of the latter race have reached a stage quite as advanced as that of any representative of the colored races" (p. 197).

In our data, although histories of natio-racial descent were not secured, it was possible to make some rough appraisals of the trait incidence in several groups by classifying subjects according to family name and hair color. This was done with the H.H.S. students, for whom the conditions of data collection were more uniform than with the M.F.S. group. Subjects were used in this treatment only if the family name belonged almost unmistakably to one or another nationality. A small number of Negro pupils were also considered as a separate group.

We believe (from general knowledge and observation) that the Italian and Irish groups in this country have undergone relatively less natio-racial mixture than many other groups. We have accordingly classified them separately, and have grouped the other families so as to yield the classes tabulated in Table II.

The subjects of Irish derivation appear to have less mid-digital hair than do other North Europeans, and the Italian subjects have even less, especially if they are dark-haired. Our limited data on Negroes are in accord with those of Danforth in showing little mid-digital hair. Although a classification based only upon family names and hair color admittedly lacks rigor, the expected effect of inaccuracies in grouping would be to obscure rather than accentuate natio-racial differences. The differences which do emerge as statistically significant, therefore, are probably real ones, and suggest the desirability of further study.

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Combination Patterns and Symmetry

Our H.H.S. cases were examined for combination of fingers bearing mid-digital hair. For simplicity only the left hands were tabulated.

In 140 of 151 affected cases, i.e. in 92.7 per cent, the combinations reported by Danforth as most frequent were found to hold. The distribution of all cases showed:

No. of affected fingers	Fingers affected	Percentage Incidence in 219 cases
0		31.0
1	4th	16.0
2	3rd, 4th	14.2
3	3rd, 4th, 5th	28.8
4	2nd, 3rd, 4th, 5th	5.0
	other combinations	5.0

In six of the 11 cases in which the left hand bore mid-digital hair in an atypical combination, the right hand was in accord with the "combination rule." In the 16 cases in which one or both hands bore mid-digital hair contrary to the combination rule, 13 were asymmetrical with respect to right and left hand.

Danforth states that in about nine out of ten cases the two hands of one person were found to be affected similarly with mid-digital hair (p. 194). Our H.H.S. indices of symmetry were found to be 92 per cent for presence or absence of hair (or follicles); but the percentage of these cases in which the two hands were found to be affected in exactly the same combination was lower, i.e. 74 per cent. Out of 56 subjects showing asymmetry, 13 or 23 per cent had at least one hand in which the mid-digital hair distribution deviated from the combination rule.

It is of course possible, (and even strongly suggested by our age data), that cases departing from the combination rule or from symmetry are mainly those from which hair and evidence of follicles have disappeared from certain fingers.

Tests for Monomeric Inheritance and Dominance

Family data. The M.F.S., H.H.S. and Supplementary family data provide 36 family groups that can be used for analying F_1 ratios for various parental combinations. The results are shown in Table III.

The incidence, q, of the allele (or combined alleles) for the condition assumed to be recessive has been estimated by calculating the square root of the proportion of non-affected individuals (in the total family population of parents and offspring combined). Cases asymmetrical in the two hands with respect to affected and non-affected conditions and cases contrary to the combination rule have not been used in the treatment which follows. Since there is not a sufficient number of matings representing all the combinations of affected and non-affected fingers, it has been necessary to make certain phenotypic groupings, viz. any fingers affected *vs.* none affected; 4, 3, or 2 fingers affected *vs.* 1 or none affected; 4 or 3 fingers affected *vs.* 2, 1, or none affected. If Danforth's conclusion that "the presence of hair in almost any degree is generally dominant over all conditions representing less amounts" (p. 198) is valid, such groupings should provide a sound test of monomeric inheritance even if two or more alleles should be lumped together in classifying affected and non-affected individuals. Such data might, on the other hand, provide evidence with respect to Danforth's alternative hypotheses accounting for the phenomenon "through the action of one or more recessive genes, or of one primary gene with several modifying factors that regulate the distribution of hair when it is present" (p. 199).

Inspection of Table III would at first suggest that a monomeric hypothesis is untenable, since matings between two "non-affected" parents produce an appreciable number of affected offspring, especially when no finger or one finger affected are presumed to be the recessive conditions. It is relevant to recall, however, the age-decrease in the incidence of mid-digital hair which we found in women over 22 years of age. This would mean that some of the mothers recorded as non-affected are probably affected genotypes. By way of interest we calculated the probable number of genotypically affected mothers included in the "non-affected" matings, on the assumption that the true proportion of affected mothers is the same as the observed

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MID-DIGITAL HAIR ON FINGERS OF TWO MEN

Figure 4

A—fingers 3, 4 and 5 carry mid-digital hair; *B*—mid-digits of fingers 3 and 4 are sparsely haired. All of the basal joints carry hair or hair follicles. See Figure 5. (The authors wish to acknowledge with appreciation the cooperation of the Department of Zoology, Columbia University

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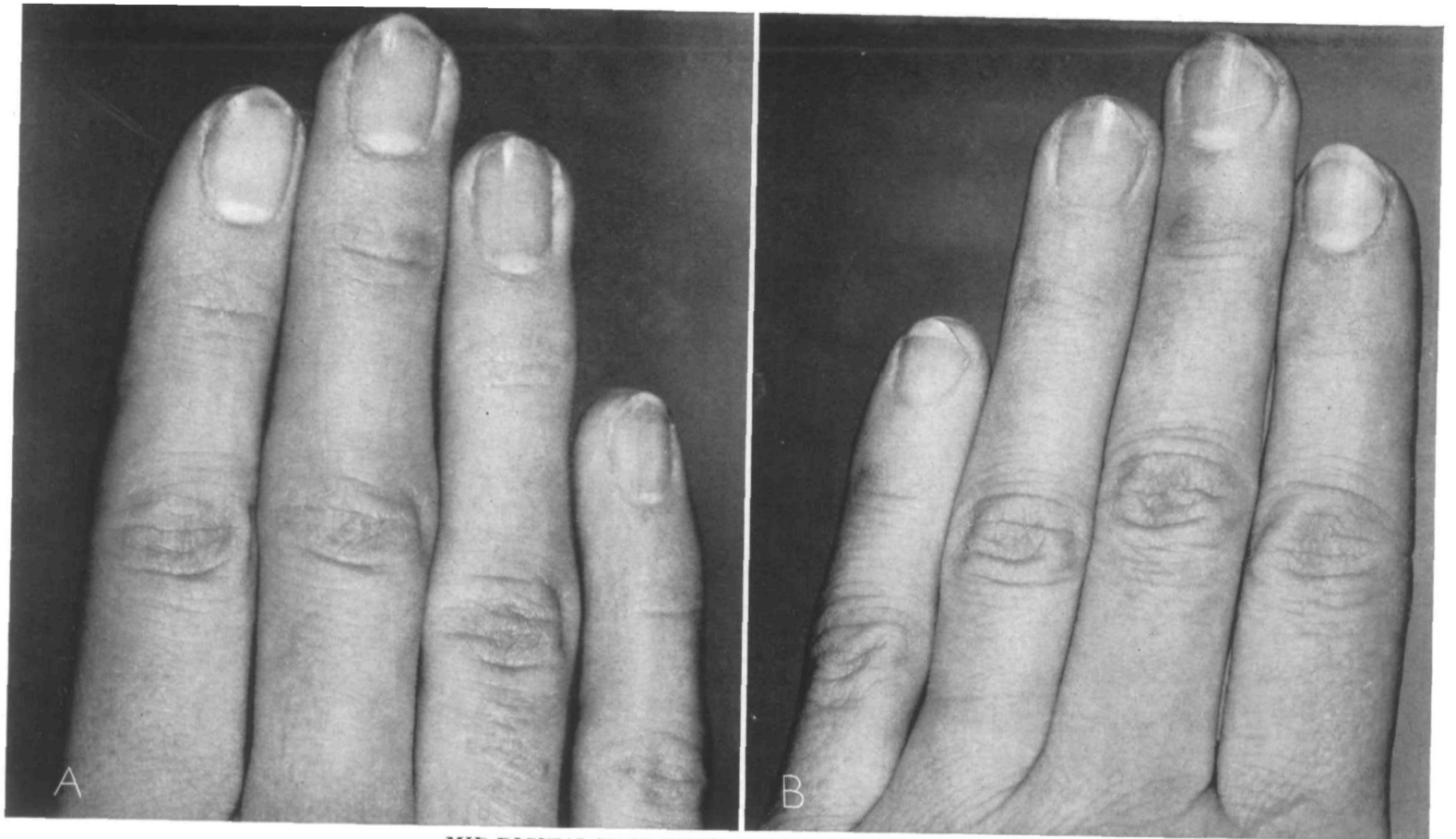

MID-DIGITAL HAIR ON FINGERS OF TWO WOMEN

Figure 5

A—fingers 3, 4 and 5, show mid-digital hair follicles but the hair has been rubbed off; *B*—all fingers show absence of mid-digital hair or of hair follicles. These four figures show several patterns of distribution of hair on the fingers of four individuals. All four fingers of the two men show hair on the basal segments. The two females show only hair follicles on these segments in the photographs, although rudimentary hair could be detected in examination of the actual fingers. The hair is lost earlier on the fingers of women than of men, but the follicles remain.

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proportion of affected fathers. The number of such cases (entered in Table III) is clearly just about sufficient to account for the affected offspring appearing contrary to Mendelian expectation.

In the matings of two affected parents, where there is no question of affected mothers failing to show up, only the presence *vs.* absence of mid-digital hair comparison provides sufficient cases for calculating expected affected and non-affected offspring. The agreement between expectation and observation is seen to be high.

In the matings which include one affected parent the observed and expected offspring ratios show fairly close agreement. As with "both parents non-affected," the presence of a few genotypically affected mothers who are classified as non-affected would tend toward an excess of affected offspring, but a slight error in the other direction due to omitting asymmetrical offspring has more weight in these matings than in the other matings. The net result is a slight excess of non-affected cases.

Sibling data. In order to utilize the larger series of H.H.S. data which included sibling pairs, but not their par-

TABLE I. Effect of Age and Sex on Incidence of Mid-digital Hair (Offspring generation of N.F.S. and H.H.S. families, right hand)

Age	No.	Proportion of indiv. affected	Standard error of prop.	Average no. affected fingers per indiv.
Under 14				
Males	25	.56	.10	.96
Females	24	.50	.10	.96
14-17				
Males	25	.52	.10	.88
Females	41	.51	.08	1.07
Under 18 (total)				
Males	50	.54	.07	
Females	65	.51	.06	
18-21				
Males	28	.57	.09	1.11
Females	23	.48	.10	.96
Over 21 (to 39)				
Males	21	.48	.11	1.00
Females	31	.19	.07	.26

TABLE II. Mid-digital Hair by Ratio-racial Groups and Hair Color (H.H.S. data)

Group	No. of lh-digitals	Proportion of indiv. affected	Standard error of prop.	Av. no. of affected fingers (Left hand)
North European				
All cases	111	.78	.04	1.97
Cases with light hair or having light-haired sib.	63	.79	.05	2.08
Irish sub-group*	38	.55	.06	1.37
Italian				
All cases	58	.55	.06	1.36
Cases with dark hair and having dark-haired sib.	27	.43	.08	1.16
Negro	8	.12		.03**
Hair color (matched to standard chart)***				
Blond	87	.75	.06	2.07
Light medium	41	.76	.07	1.68
Dark medium	37	.74	.06	1.88
Dark	83	.64	.06	1.34

* N.F.S. offspring generation cases were included in order to secure more cases for comparison.

** Only one of the eight Negro pupils had mid-digital hair, and on only the 4th fingers.

*** Only white subjects were used for this comparison.

TABLE III. Offspring Phenotypes in Mid-digital Hair for Three Types of Matings (H.H.S., N.F.S., Suppl. families.

"Affected" have hair on fingers:	PARENTAL COMBINATIONS: Both P affected — Offspring: Aff.	Non-aff.	Omitted	One P affected — Offspring: Aff.	Non-aff. Obs.	Non-aff. Exp.	Omitted	Both P non-affected — Offspring: Aff.	Non-aff.	Omitted	Estimated combined genotypes responsible for non-affected phenotype.
2,3,4,5 * or 3,4,5	4	— (2 families)	—	15	17 (9 families)	15.3	4	3	109 (23 families) 1 mother may be aff.	1	$A_2 A_1^A{}_0$ .917
2,3,4,5 ** 3,4,5 or 3,4	11	4 (4 families)	—	17	21 (12 families)	17.2	7	10	58 (16 families) 3-4 mothers may be affected.	4	$A_1^A{}_0$ .889
2,3,4,5 *** 3,4,5 3,4 or 4 only	45	8 Obs. 9.0 Exp. (12 families)	3	22	17 (12 families)	16.1	7	7	47 (12 families) 3 mothers may be aff.	1	$A^A{}_0$ .704

* Affected mothers are 3 per cent fewer than affected fathers.

** 23 per cent fewer affected mothers. There are four families included in the other phenotype comparisons which could not be here included because of parents failing to meet our "symmetry" criterion with respect to affected and non-affected conditions.

*** 24 per cent fewer affected mothers.

TABLE IV. Tests of Monomeric Inheritance and Dominance of Mid-digital Hair over Absence or Lesser Degrees of Mid-digital Hair. (H. H. S. siblings.)

Phenotypic contrast	No. of subjects	Estimated q	Affected members of sibling pairs	Pairs observed	Pairs expected	Random no. pairs expected	Monomeric hypoth. chi-square	Monomeric hypoth. P (approx.) (for df)	Random distribution hypoth. chi-square	Random distribution hypoth. P (for n=2)
I D: $A_4 A_3 A_2 A_1$ R: A_0 15 sibships omitted	187 47	.5195	0 1 2	14 19 54	13.4 19.8 53.6	6.3 34.3 46.4	.047	.8	17.4	<.01
II D: $A_4 A_3 A_2$ R: $A_1 A_0$ 18 sibships omitted	84 54	.7071	0 1 2	29 26 29	30.6 22.8 30.6	21.0 42.0 21.0	.6168	.5	12.1	<.01
III D: $A_4 A_3 A_2$ R: $A_1 A_0$ Atypical cases added (16 prs.) 2 sibships omitted	112 88	.6533	0 1 2	29 30 41	30.4 27.1 42.4	19.4 49.3 31.3	.4210	.6	15.3	<.01
IV D: $A_4 A_3$ R: $A_2 A_1 A_0$ 27 sibships omitted	51 99	.8124	0 1 2	39 21 15	40.6 17.7 16.7	32.7 32.6 8.7	.8815	.4	10.5	<.01
V D: $A_4 A_3$ R. $A_2 A_1 A_0$ Atypical cases added (22 prs.) 5 sibships omitted	84 106	.7481	0 1 2	39 30 22	41.1 25.8 30.2	30.0 48.0 19.0	.9513	.3	13.6	<.01

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ents, a method presented by Cotterman was applied. When data comprising only a single generation are available, it is possible to test for inheritance through a single dominant gene substitution by a comparison of observed and expected frequencies of sibling pair combinations. In the present instance the use of this method has the distinct advantage that the older subjects (i.e. the parents and particularly the mothers), some of whose phenotypes have changed with age, can be disregarded.

For the case of two sibs per family, the expected percentages of sibling phenotypic combinations are:

Both dominant $\frac{1}{4}\ p\ (4 + 5p - 6p^2 + p^3)$
One dominant $\frac{1}{2}\ p\ (1-p)^2\ (4-p)$
Both recessive $\frac{1}{4}\ (1-p)^2\ (2-p)^2$

where p is the incidence of the dominant gene.

Only white families were used, and only two siblings per family. In the families having more than two children examined, the two older children were arbitrarily selected for this comparison. Cases were omitted when the combinations of fingers bearing mid-digital hair were contrary to the "combination rule," or when one hand showed the affected and the other hand the non-affected phenotype. The numbers of siblings thus omitted are shown in Table IV.

There is marked agreement between observed and expected frequencies of sibling pair combinations, the chi-square test showing the deviations to be within ordinary chance range.*

As in the previous test based on parents and offspring, certain phenotypic groupings were necessary to insure an adequate number of sibling pairs. Thus in the first comparison, the presence of hair on 1, 2, 3, or 4 fingers was assumed to be dominant (D) over recessive absence of hair (R). In the second comparison the presence of hair on 2, 3, or 4 fingers was assumed to be dominant over absence of hair on only one finger. In the fourth comparison, hair on 3 or 4 fingers was assumed to be dominant over 0, 1, or 2 affected fingers.

In the third and fifth comparisons cases previously excluded on the ground of asymmetry or failure to agree with the combination rule were added and classified with the four or three affected fingers group if at least one hand had finger 5 affected (with hair; not with follicles alone); with the two or more affected fingers group if at least one hand had hair on fingers 3 or 5 or both. Our preliminary study of affected finger combinations had shown that if finger 5 was affected, fingers 3 and 4, or 2, 3 and 4 were in general affected also. It therefore seemed legitimate to test the assumption that certain atypical cases were genetically equivalent to typical cases. It is seen that when sibling pairs containing atypical cases as defined are added the agreement between observation and expectation is about as good as when these pairs are not used. Further investigation would be necessary, however, before we could equate the atypical cases to the typical ones with any assurance.

Returning, now, to the hypotheses which have been considered to account for mid-digital hair, we believe the evidence favors monomeric rather than polymeric inheritance, and that the dominance of hair in almost any degree over lesser amounts occurs too regularly to

*It may be noted however, that the deviations tend to be in the same direction for most of the corresponding comparisons, e.g. that the expected frequency of pairs with one affected and one non-affected member tends to be lower than the observed. It may be supposed that this is a consequence of estimating q (and $p = 1\text{-}q$) from the proportion of non-affected individuals, some of whom may actually be affected genotypes. Errors in diagnosing the affected condition would result in underestimating p, which in turn would have more influence upon the calculated expectation for pairs with one affected member than upon the other calculated expectations, a fact evident from the formulae. The question may be raised as to why p estimated from chi-square is given on the basis of only one degree of freedom when there are three pairs of entries corresponding to each estimate. Cotterman, p. 129, explains the loss of two degrees of freedom in accordance with the fact that the expected frequencies have been adjusted to agree with the observed series in two respects, i.e. their total number and the proportion of recessives from which the gene frequency is estimated.

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be compatible with a hypotheses of a single main gene substitution with modifiers regulating distribution.

A Multiple Allele Hypothesis

One of us (Bernstein) has envisaged a hypothetical series of alleles A_1, A_2, A_3, A_4 (in order of increasing dominance) with subscripts corresponding to the number of fingers affected with mid-digital hair, and A_0 in homozygous condition corresponding to absence of mid-digital hair. We do not have sufficient data to make separate tests for the presence of each of these alleles and in particular our data do not permit a satisfactory test to distinguish between A_3, A_4. The A_3 and A_4 conditions are clearly differentiated, however, from the other conditions, both in the family data classified by matings, and in the H.H.S. sibling data. It is possible that A_3 and A_4 are sometimes genetically equivalent and sometimes overlapping, since Danforth not only reports two A_4 siblings whose parents are both A_3 but also reports far more offspring who are not A_4, though having an A_4 parent, than would be compatible with a separate A_4 allele. In our own data we also have two A_4 siblings whose parents are both A_3, which raises the question of A_4 sometimes representing a homozygous condition of A_3. But we also have three families with A_4 offspring in which the father is A_4, and one family with an A_4 child in which the mother is A_3, the father A_1, which again raises the question of inadequate diagnosis of older females.

As a further check we took all A_4 subjects of offspring generation from the family data and H.H.S. siblings, and computed the proportion of A_4 cases among their siblings. Each family was used as often as it contained A_4 cases, so that the expected proportions of affected siblings assuming A_4 to be a rare dominant, would be 50 per cent. The result of this examination gave 18 A_4 offspring whose 29 siblings included 10 or 34 per cent A_4 cases, and 11 or 38 per cent A_3 cases.

Aside from the question of an A_3, A_4 distinction, our H.H.S. sibling data are consistent with a hypothetical A_4 or A_3, A_2, A_1, A_0, and our family data are consistent if appropriate allowance is made for genotypically affected mothers occurring as non-affected phenotypes.

Summary and Conclusions

In a study of the distribution of mid-digital hair in man with especial reference to problems opened by Danforth's previous study:

1. No significant difference in sex incidence was found in subjects under 18 years of age. The males showed no marked age trend after this age, but the females showed a decided drop in affected cases after age 21. This result is interpreted both in terms of the higher incidence in females of very rudimentary hair and their more frequent performance of manual work (housework), which may wear away mid-digital hair and obliterate the follicles.

2. Subjects of Irish derivation appear to have less mid-digital hair than do other North Europeans, and Italians have even less, especially if they are dark-haired. Our limited data on Negroes are in accord with those of Danforth in showing little mid-digital hair.

3. The combinations of 1, 2, 3, and 4 affected fingers reported by Danforth as most frequent were found to hold with few exceptions in the present data. The proportion of our cases (of high school age) whose two hands were affected symmetrically was 74 per cent, as compared with about 90 per cent in Danforth's groups. There is reason for believing that hands departing from the "combination rule" are phenotypic deviates, since in nearly all such cases the right and left hand are asymmetrical with respect to each other.

4. Danforth's finding that with very few exceptions a child will have mid-digital hair on no more fingers than its more hairy parent was confirmed. One of the authors (Bernstein) offers a multiple allelomorph hypothesis, A_0, A_1, A_2, A_3, A_4 to account for distinction of the hair on the digits. If A_3 and A_4 are in fact separate alleles, there appears to be phenotypic overlapping. Aside from this distinction, our two generation pedigrees are consistent with the multiple allele

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hypothesis if appropriate allowance is made for genotypically affected mothers occurring as non-affected phenotypes. Again ignoring the A_3, A_4 distinction, our single generation results on siblings of high school age, examined by Cotterman's method of testing for monomeric inheritance with dominance, are even more consistent with the multiple allele hypothesis.

5. In view of the excellent agreement with Mendelian theory obtained from siblings showing regularity in the distribution of mid-digital hair, but the difficulty experienced in diagnosing certain cases, particularly among mature women and among infants, it would be desirable in order to facilitate use of this trait in human genetics work to pursue further research upon the conditions that permit rigorous classification of the pilosity of subjects.

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A CASE OF VIABLE TWIN CHICKS

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THE recent reviews of twinning in this Journal by Newman[1] and Waddington[2] make it seem desirable to report a case of twin chicks which lived for a short time after hatching. The case seems to be of sufficient rarity to merit a brief description.

The twins (of the Austra-White breed) were hatched on July 15, 1941, at Pettys' Hatchery near Urbana, Illinois, and the following information was given to the author by Mr. Pettys a few days after the event had occurred. During the routine removal of newly-hatched chicks from incubator trays, one chick (referred to as No. 2 below) was noticed to have almost emerged from an egg. With some help this chick freed itself from the shell, and a second chick (No. 1) was noticed on the bottom of the egg shell. According to Mr. Pettys there is no doubt that both chicks emerged from the same shell. No. 2 seemed healthy and capable of moving around freely, in spite of the fact that the toes on the left foot were crooked (Figure 6*A*). Both chicks were fully covered with down and No. 2 showed fairly well-developed primary wing feathers. No. 1 could not stand due to the fact that the right leg was "deformed." This chick died when it was 24 hours old and I did not see it alive, while No. 2 was still alive two days after hatching. It appeared normal in all respects except size (Figure 6*B*). It died when it was two days old. Both dead chicks were made available to me for inspection soon after the second chick died. Even though the dead chicks had been kept in the refrigerator they were in the beginning stages of decomposition. The chicks were weighed and autopsied. No. 1 weighed 11 grams. No. 2 weighed 16 grams. Because the weight of the chick is positively correlated with the weight of the egg, one would expect normal chicks of the Austra-White breed to weigh from 35 to 45 grams at hatching. The viscera appeared normal by inspection but could not be removed from the birds without tearing because of beginning decomposition and no comparative

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