

THE OHIO JOURNAL OF SCIENCE

VOL. XXXVII

MAY, 1937

No. 3

INDICATION OF UNIT FACTOR INHERITANCE IN DATA COMPRISING BUT A SINGLE GENERATION

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It has been shown by Penrose (1935) that linkage between two autosomal unit characters can be detected and measured through the investigation of randomly collected pairs of brothers and sisters of unspecified parentage. This discovery promises to be of great assistance to university laboratories and similar institutions where parents are secured with difficulty. It should also prove of interest if from data of the same sort it were possible to test the hypothesis of unit factor inheritance for any human trait, and it would seem worth while, in this event, to apply such a test to both traits under investigation before proceeding with the analysis of linkage between them. Such a test, it is thought, may be accomplished by the methods to be described in this note.

Let us suppose that two characters, which we shall simply designate (+) and (-), are thought to be determined by a single pair of autosomal genes, T and t, with (+) being the dominant character. Randomly collected sibships whose parents have not been ascertained may readily be classified as to their composition and the number of each sort recorded. Now, if the population be assumed at equilibrium with respect to the distribution of genes T and t, a condition which must necessarily follow the occurrence of random mating, we may then estimate the frequencies of the two alleles. From these we may calculate the expected frequencies of the various sorts of sibship and measure the discrepancy between calculated and observed values by the usual Chi-square (χ^2) test.

USE OF SIB-PAIRS

One procedure, which has the advantage of entailing a minimum of calculations, consists in the classification of all sib-pairs

contained in the available sibships of larger size and adding these numbers to those obtained from sibships of only two members. In general, a sibship of s members must supply ${}^sC_2 = s(s-1)/2$ sib-pairs. However, since a χ^2 -test of sibships in which the expected number in any class is less than 5 must suffer considerable inaccuracy, it is therefore advisable to exclude sibships of such sizes, rather than allow these to contribute to the three classes of sib-pairs.

Designating the frequencies of genes T and t by p and $(1-p)$, respectively, the expected proportions of sib-pairs having 0, 1, and 2 members showing the (+) character may be deduced by

TABLE I

| Type of Sib-pair | Possible Genotypes of Parents | Proportional Frequency of Mating | Probability of Sib-pair | Expected Proportion of Sib-pairs |
|--|----------------------------------|----------------------------------|-------------------------|----------------------------------|
| Both (-) (tt, tt) | $Tt \times Tt$ | $4p^2(1-p)^2$ | $\frac{1}{16}$ | $\frac{1}{4} p^2(1-p)^2$ |
| | $Tt \times tt$ $tt \times tt$ | $\frac{4p(1-p)^3}{(1-p)^4}$ | $\frac{1}{4}$ 1 | $\frac{p(1-p)^3}{(1-p)^4}$ |
| (+ and -) (TT, tt) or (Tt, tt) | $Tt \times Tt$ | $4p^2(1-p)^2$ | $\frac{1}{16}$ | $\frac{3}{2} p^2(1-p)^2$ |
| | $Tt \times tt$ | $4p(1-p)^3$ | $\frac{1}{2}$ | $2p(1-p)^3$ |
| Both (+) (TT, TT) or (TT, Tt) or (Tt, Tt) | $TT \times TT$ | p^4 | 1 | p^4 |
| | $TT \times Tt$ | $4p^3(1-p)$ | 1 | $4p^3(1-p)$ |
| | $TT \times tt$ | $2p^2(1-p)^2$ | 1 | $\frac{2p^2(1-p)^2}{9}$ |
| | $Tt \times Tt$ | $4p^2(1-p)^2$ | $\frac{1}{16}$ | $\frac{1}{4} p^2(1-p)^2$ |
| | $Tt \times tt$ | $4p(1-p)^3$ | $\frac{1}{4}$ | $p(1-p)^3$ |

application of the principle of random mating as is shown in Table I. The expectations in the three classes are found by summing the terms in the extreme right-hand column for each type of sib-pair. In a sample of n_2 sib-pairs the expected frequencies of sib-pairs having 0, 1, and 2 (+) members are therefore, respectively,

$$\left. \begin{aligned}
 f_{20} &= \frac{1}{4}(1-p)^2(2-p)^2n_2, \\
 f_{21} &= \frac{1}{2}p(1-p)^2(4-p)n_2, \\
 \text{and } f_{22} &= \frac{1}{4}p(4+5p-6p^2+p^3)n_2.
 \end{aligned} \right\} \dots\dots\dots(1)$$

The most convenient means of obtaining an estimate of p is by employing the observed proportions of (+) and (-) individuals in the aggregate of the sibships used in the χ^2 -test. The expected proportions of (+) and (-) individuals under random mating are $1-(1-p)^2$ and $(1-p)^2$, respectively, and if the corresponding observed proportions are A and B , we may then take

$$p = 1 - \sqrt{B} \dots \dots \dots (2)$$

Using this estimate we may calculate the expected frequencies (1) of the three sib-pair types and compare these with the observed numbers by the method of Chi-square. The number of degrees of freedom to use in entering a probability table of χ^2 values is one (1) in this case, in accordance with the fact that the expected values are adjusted so as to conform with the observed series in two respects—the total number, n_2 , and the parameter, p .

TABLE II

| Type of Sibship | Possible Genotypes of Parents | Proportional Frequency of Mating | Probability of Sibship | Expected Proportion of Sibships |
|---|-------------------------------|----------------------------------|--|---|
| All s (-) $s(tt)$ | Tt × Tt | $4p^2(1-p)^2$ | $(\frac{1}{4})^s$ | $4(\frac{1}{4})^s p^2(1-p)^2$ $4(\frac{1}{2})^s p(1-p)^3$ $(1-p)^4$ |
| | Tt × tt | $4p(1-p)^3$ | $(\frac{1}{2})^s$ | |
| | tt × tt | $(1-p)^4$ | 1 | |
| r (+), $s-r$ (-) $r(TT, Tt)$ $s-r(tt)$ | Tt × Tt | $4p^2(1-p)^2$ | ${}^s C_r (\frac{3}{4})^r (\frac{1}{4})^{s-r}$ | $4 {}^s C_r (\frac{3}{4})^r (\frac{1}{4})^{s-r} p^2(1-p)^2$ $4 {}^s C_r (\frac{1}{2})^s p(1-p)^3$ |
| | Tt × tt | $4p(1-p)^3$ | ${}^s C_r (\frac{1}{2})^s$ | |
| All s (+) $s(TT, Tt)$ | TT × TT | p^4 | 1 | p^4 $4p^3(1-p)$ $2p^2(1-p)^2$ $4(\frac{3}{4})^s p^2(1-p)^2$ $4(\frac{1}{2})^s p(1-p)^3$ |
| | TT × Tt | $4p^3(1-p)$ | 1 | |
| | TT × tt | $2p^2(1-p)^2$ | 1 | |
| | Tt × Tt | $4p^2(1-p)^2$ | $(\frac{3}{4})^s$ | |
| | Tt × tt | $4p(1-p)^3$ | $(\frac{1}{2})^s$ | |

USE OF SIBSHIPS OF LARGER SIZE

A more extensive treatment of the data might be undertaken by comparing the observed frequencies of the various sorts of trios, quartettes, quintettes, etc., with the frequencies expected under random mating. In general, for sibships of size s , the expected proportions of each of the $(s+1)$ different sorts may be derived as shown in Table II. The expected frequencies in the three classes indicated in the table are found by summing

the terms in the right-hand column for each class and multiplying by n_s , the observed number of sibships of s . The expected number of sibships having all s members of the (+) type is

$$f_{ss} = \{ p^4 + 4p^3(1-p) + (2+3^s4^{1-s})p^2(1-p)^2 + 2^{2-s}p(1-p)^3 \} n_s, \tag{3}$$

and the expected number having no (+) members is

$$f_{s0} = \{ 4^{1-s}p^2(1-p)^2 + 2^{2-s}p(1-p)^3 + (1-p)^4 \} n_s \\ = \left\{ (1-p) \left[1 - p \left(\frac{2^{s-1}-1}{2^{s-1}} \right) \right]^2 \right\} n_s, \tag{4}$$

while for the remaining $(s-1)$ types, the expectations can be calculated from the expected number of sibships having r (+) and $s-r$ (-) members,

$$f_{sr} = \{ 4^s C_r \left(\frac{3}{4}\right)^r \left(\frac{1}{4}\right)^{s-r} p^2(1-p)^2 + 4^s C_r \left(\frac{1}{2}\right)^s p(1-p)^3 \} n_s \\ = {}^s C_r p(1-p)^2 \left\{ p \frac{3^r}{4^{s-1}} + (1-p) \frac{1}{2^{s-2}} \right\} n_s, \tag{5}$$

which is general except for the cases, $r=0$ and $r=s$.

TABLE III

Polynomials for Computing the Expected Proportions of Various Sibship Classes

| Class | | Coefficient of | | | | |
|-------|---|----------------|------|----------------|----------------|----------------|
| s | r | 1 | p | p ² | p ³ | p ⁴ |
| 2 | 0 | 4 | -12 | 13 | -6 | 1 |
| 2 | 1 | | 8 | -18 | 12 | -2 |
| 2 | 2 | | 4 | 5 | -6 | 1 |
| 3 | 0 | 16 | -56 | 73 | -42 | 9 |
| 3 | 1 | | 24 | -63 | 54 | -15 |
| 3 | 2 | | 24 | -45 | 18 | 3 |
| 3 | 3 | | 8 | 35 | -30 | 3 |
| 4 | 0 | 64 | -240 | 337 | -210 | 49 |
| 4 | 1 | | 64 | -180 | 168 | -52 |
| 4 | 2 | | 96 | -234 | 180 | -42 |
| 4 | 3 | | 64 | -84 | -24 | 44 |
| 4 | 4 | | 16 | 161 | -114 | 1 |
| 5 | 0 | 256 | -992 | 1441 | -930 | 225 |
| 5 | 1 | | 160 | -465 | 450 | -145 |
| 5 | 2 | | 320 | -870 | 780 | -230 |
| 5 | 3 | | 320 | -690 | 420 | -50 |
| 5 | 4 | | 160 | -75 | -330 | 245 |
| 5 | 5 | | 32 | 659 | -390 | -45 |

Expressions (3), (4), and (5) are polynomials in p of the 4th degree. For the purpose of simplifying calculations the coefficients of each term have been computed and set out in Table III for the various sorts of sibships of 2, 3, 4, and 5 members. The expected frequency in any class may be found by summing the terms containing the appropriate coefficients, dividing the sum by the quantity, $2^{2(s-1)}$, and multiplying by the total number of sibships of that size. For example, the expected number of trios having 1 (+) member and 2 (-) members is

$$f_{31} = \frac{n_3}{16}(24p - 63p^2 + 54p^3 - 15p^4).$$

Separate estimates of p may be calculated from the proportions of (+) individuals among sibships of each size or a single estimate may be obtained from the proportion found among sibships of all sizes. In the first case, a χ^2 -test of sibships of size s will involve $s-1$ degrees of freedom and χ^2 may thus be calculated for each size of sibship separately. When a single value of p is used χ^2 may be calculated for the entire data and the number of degrees of freedom will be one less than the sum of all values of s .

ALTERNATIVE HYPOTHESES

An important limitation of the method described above is the fact that, except for very extensive data, it should not generally be possible to distinguish whether (+) or (-) is actually the dominant trait, even when the hypothesis of unit factor inheritance has been confidently established. This may be demonstrated in a general way as follows: If, instead of assuming (+) to be the dominant character as in the above analysis, we should assume (+) to be the recessive trait, than we might estimate the frequency of the dominant gene as

$$p' = 1 - \sqrt{A}, \dots\dots\dots (6)$$

and the expected frequencies of sibships of 0, 1 and 2 (+) members would then be the reverse of those given in (1), that is,

$$\left. \begin{aligned} f'_{20} &= \frac{1}{4}p'(4 + 5p' - 6p'^2 + p'^3)n_2, \\ f'_{21} &= \frac{1}{2}p'(1 - p')^2(4 - p')n_2, \\ f'_{22} &= \frac{1}{4}(1 - p')^2(2 - p')^2n_2, \end{aligned} \right\} \dots\dots\dots (7)$$

or, substituting the estimate p' given by (6),

$$\left. \begin{aligned} f'_{20} &= \left\{ 1 - \frac{1}{2}A(1 - \sqrt{A}) (3 + \sqrt{A}) - \frac{1}{4}A(1 + \sqrt{A})^2 \right\} n_2, \\ f'_{21} &= \frac{1}{2}A(1 - \sqrt{A}) (3 + \sqrt{A}) n_2, \\ f'_{22} &= \frac{1}{4}A(1 + \sqrt{A})^2 n_2. \end{aligned} \right\} \dots (8)$$

These are to be compared with

$$\left. \begin{aligned} f_{20} &= \frac{1}{4}(1 - A) (1 + \sqrt{1 - A})^2 n_2, \\ f_{21} &= \frac{1}{2}(1 - A) (1 - \sqrt{1 - A}) (3 + \sqrt{1 - A}) n_2, \\ f_{22} &= \left\{ 1 - \frac{1}{2}(1 - A) (1 - \sqrt{1 - A}) (3 + \sqrt{1 - A}) - \frac{1}{4} \right. \\ &\quad \left. (1 - A) (1 + \sqrt{1 - A})^2 \right\} n_2, \end{aligned} \right\} \dots (9)$$

the values expected where (+) is dominant, found by putting $p = 1 - \sqrt{1 - A}$ in the expressions in (1).

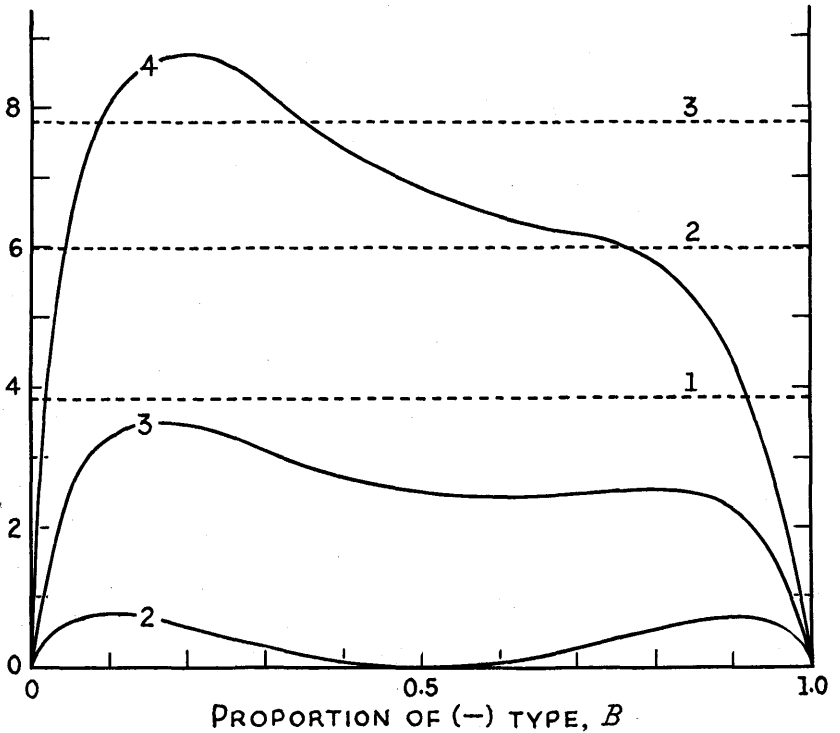


FIG. 1. Expected values of χ^2 as a measure of discrepancy between sibship expectations under the assumptions of dominance of (+) and of (-) types, calculated on the basis of 100 sibships each of 2, 3, and 4 sibs. Compare with the 5 per cent levels of significance for 1, 2, and 3 degrees of freedom, shown by broken lines.

We may get some idea as to the relative chances of eliminating the hypothesis of dominance for the (-) trait by assuming the observed frequencies to be consistent with the expectations of dominance for the (+) trait and by calculating the expected value of χ^2 as a measure of the discrepancies between corresponding expectations under the two hypotheses. The quantity,

$$\chi^2 = S \left\{ \frac{(f'_{sr} - f_{sr})^2}{f'_{sr}} \right\},$$

is plotted in Figure 1 for values of B from 0 to 1 and for sibships of two, three, and four members, using 100 sibships of each size. The results show that sibships of larger size are more valuable in attempting to discriminate between the two hypotheses, but that considerably larger numbers should be available even in these cases.

TABLE IV

Expected values of χ^2 as a measure of discrepancy between sib-pair expectations under the assumptions of unit factor inheritance with (+) as the dominant trait and of non-genetic chance determination, calculated on the basis of 100 sib-pairs.

| Proportion of (-) type, B | χ^2 | Proportion of (-) type, B | χ^2 |
|-----------------------------------|----------|-----------------------------------|----------|
| 0 | 0 | 0.6 | 21.89 |
| 0.1 | 13.77 | 0.7 | 22.95 |
| 0.2 | 16.40 | 0.8 | 23.64 |
| 0.3 | 18.29 | 0.9 | 24.34 |
| 0.4 | 19.76 | 1.0 | 0 |
| 0.5 | 20.92 | | |

In the investigation of a trait heretofore unstudied from the genetic standpoint it might be desirable to eliminate, if possible, another hypothesis, namely, that the difference between (+) and (-) types is attributable to chance agencies in which biological relationship plays no part. Under this supposition, however, we should expect the various sorts of sibships of s to occur with frequencies which are the terms in the expansion of the binomial,

$$(A + B)^s n_s.$$

Comparing these expectations with those based upon the assumption of unit factor inheritance by calculating χ^2 as before we have the values listed in Table IV, in which 100 sibships of two members are assumed to be available. The table shows

that we may be quite confident of eliminating an hypothesis of non-genetic chance determination if the data are, in fact, consistent with expectations under the hypothesis of unit factor inheritance.

APPLICATION TO DATA ON "P. T. C." TASTE DEFICIENCY

For the purpose of illustrating the χ^2 -test of sibships by a numerical example, we may test a body of data on phenylthiocarbamide taste deficiency. Crystals of "P. T. C." were used in making these tests, and most of the families recorded consisted of sibs whose parents were not tested. Utilizing those families in which both parents were tested, however, we may, as a preliminary measure, test the hypothesis of random mating with respect to this character. A simple procedure for this purpose consists in the use of a two-by-two table in which members of either sex are classified as to their own taste reactions and as to the taste reactions of their mates. A significant deviation from proportionality in the four combination classes may then be taken as indicative of assortative mating or the absence of random mating.

Since ability to taste has previously been shown (Blakeslee and Salmon, 1931; Snyder, 1931) to be the dominant trait, we may designate tasters by (+) and non-tasters by (-). In the 78 families having both parents tested the observed frequencies of the four parental combinations are as shown in the following table:

TABLE V

| | | | |
|------------|----|-------|-----------|
| 43 | 17 | 60 | + } wives |
| 13 | 5 | 18 | |
| 56 | 22 | 78 | } total |
| + - | | | |
| } husbands | | total | |

The entries are almost exactly proportional to the marginal frequencies as should be expected under random mating. The value expected in the class in which both parents are non-tasters is $(22 \times 18) / 78 = 5.077$. Calculation of the probability of a departure from expectation equal to or greater than the one

observed is as follows (cf. Fisher, p. 99): The observed set of entries and those more extreme in their deviation from proportionality in the same direction are

$$\begin{bmatrix} 43 & 17 \\ 13 & 5 \end{bmatrix}, \begin{bmatrix} 42 & 18 \\ 14 & 4 \end{bmatrix}, \begin{bmatrix} 41 & 19 \\ 15 & 3 \end{bmatrix}, \begin{bmatrix} 40 & 20 \\ 16 & 2 \end{bmatrix}, \begin{bmatrix} 39 & 21 \\ 17 & 1 \end{bmatrix}, \begin{bmatrix} 38 & 22 \\ 18 & 0 \end{bmatrix},$$

and their respective probabilities are

$$\left(\frac{60!18!56!22!}{78!} \right) \left(\frac{1}{43!17!13!5!}, \frac{1}{42!18!14!4!}, \frac{1}{41!19!15!3!}, \frac{1}{40!20!16!2!}, \frac{1}{39!21!17!}, \frac{1}{38!22!18!} \right),$$

or, 0.2341, 0.1998, 0.1177, 0.0453, 0.0101, 0.0010. The observed set of entries is therefore to be expected by chance in over 23 per cent of trials and deviations from proportionality in the direction observed of equal or greater magnitude should be obtained in as much as 60 per cent of trials. The assumption of random mating is thus highly justified.

TABLE VI

Numbers of cases of various sibships of 2, 3, and 4 sibs tested for "P. T. C." taste deficiency

| Size of Sibship, s | Number of Tasters, r | | | | | Totals, n _s |
|--------------------|----------------------|----|----|----|----|------------------------|
| | 0 | 1 | 2 | 3 | 4 | |
| 2 | 11 | 22 | 74 | .. | .. | 107 |
| 3 | 8 | 8 | 16 | 38 | .. | 70 |
| 4 | 1 | 5 | 7 | 8 | 16 | 37 |

The observed frequencies of the various sorts of sibships of 2, 3, and 4 members are given in Table VI. Larger sibships were also contained in the data but were few in number and no analysis of them shall be attempted.

The total number of tasters in sibships of any size, s, is found by summing the quantity r (n_{s,r}) for all values of r. For example, among sib-pairs the total number of tasters is (0.11 + 1.22 + 2.74) = 170, the total number of individuals among sib-pairs is sn_s = 2.107 = 214, and the proportion of tasters in sibships of 2

is therefore $A = 170/214 = 0.7943925$, giving $p = 1 - \sqrt{1 - A} = 0.5466$. The values of A and p calculated in a similar manner from sibships of 3 and 4 are shown in Table VII.

TABLE VII

Values of A and p indicated by sibships of 2, 3, and 4 sibs

| Size of Sibship, s | Total Number of Tasters | Total Number of sibs, sn_s | Proportion of Tasters, A | p ($= 1 - \sqrt{1 - A}$) |
|----------------------|-------------------------|------------------------------|----------------------------|---------------------------------|
| 2 | 170 | 214 | .7943925 | .5466 |
| 3 | 154 | 210 | .7333333 | .4836 |
| 4 | 107 | 184 | .7229729 | .4737 |

TABLE VIII

Calculation of the Expected Frequencies

| Class s r | $k_0 p^0$ | $k_1 p^1$ $p = .5466$ | $k_2 p^2$ $p^2 = .2988$ | $k_3 p^3$ $p^3 = .1633$ | $k_4 p^4$ $p^4 = .0893$ | $\sum_{i=0}^4 k_i p^i$ | Expected Frequency $f_{sr} = \frac{n_s}{2^2(s-1)} \sum_{i=0}^4 k_i p^i$ |
|------------------|-----------|--------------------------|----------------------------|----------------------------|----------------------------|------------------------|--|
| 2 0 | 4 | -6.5592 | 3.8844 | - .9798 | .0893 | .4347 | 11.6282 |
| 2 1 | | 4.3728 | -5.3784 | 1.9596 | -.1786 | .7754 | 20.7420 |
| 2 2 | | 2.1864 | 1.4940 | - .9798 | .0893 | 2.7899 | 74.6298 |
| | | $p = .4836$ | $p^2 = .2339$ | $p^3 = .1131$ | $p^4 = .0547$ | | |
| 3 0 | 16 | -27.0816 | 17.0747 | -4.7502 | .4923 | 1.7352 | 7.5915 |
| 3 1 | | 11.6064 | -14.7357 | 6.1074 | -.8205 | 2.1576 | 9.4395 |
| 3 2 | | 11.6064 | -10.5255 | 2.0358 | .1641 | 3.2808 | 14.3535 |
| 3 3 | | 3.8688 | 8.1865 | -3.3930 | .1641 | 8.8264 | 38.6155 |
| | | $p = .4737$ | $p^2 = .2244$ | $p^3 = .1063$ | $p^4 = .0504$ | | |
| 4 0 | 64 | -113.6880 | 75.6228 | -22.3230 | 2.4696 | 6.0814 | 3.5158 |
| 4 1 | | 30.3168 | -40.3920 | 17.8584 | -2.6208 | 5.1624 | 2.9845 |
| 4 2 | | 45.4752 | -52.5096 | 19.1340 | -2.1168 | 9.9828 | 5.7713 |
| 4 3 | | 30.3168 | -18.8496 | -2.5512 | 2.2176 | 11.1336 | 6.4366 |
| 4 4 | | 7.5792 | 36.1284 | -12.1182 | .0504 | 31.6398 | 18.2918 |

The expected frequencies of the various sorts of sibships of 2, 3, and 4 are calculated in Table VIII. The coefficients, k_0 - k_4 , are obtained from Table III and the values of p used for each sibship size are those given in Table VII.

Two classes of quartettes (0 and 1 taster) have expected frequencies which are less than 5 and it is customary to combine such classes in the χ^2 -test, using one less degree of freedom, as shown in Table IX.

TABLE IX
Calculation of χ^2 for sibships of each size and for the total

| Class s r | Observed Frequency, n_{sr} | Expected Frequency, f_{sr} | $\frac{(f_{sr}-n_{sr})^2}{f_{sr}}$ | χ^2 | Degrees of Freedom | Proba- bility, P |
|--------------|------------------------------------|------------------------------------|------------------------------------|----------|--------------------------|------------------------|
| 2 0 | 11 | 11.6282 | .034 | .115 | 1 | .74 |
| 2 1 | 22 | 20.7420 | .076 | | | |
| 2 2 | 74 | 74.6298 | .005 | | | |
| 3 0 | 8 | 7.5915 | .002 | .441 | 2 | .80 |
| 3 1 | 8 | 9.4395 | .220 | | | |
| 3 2 | 16 | 14.3535 | .189 | | | |
| 3 3 | 38 | 38.6155 | .010 | | | |
| 4 0, 1 | 6 | 6.5003 | .039 | .968 | 2 | .62 |
| 4 2 | 7 | 5.7713 | .262 | | | |
| 4 3 | 8 | 6.4366 | .380 | | | |
| 4 4 | 16 | 18.2918 | .287 | | | |
| Totals | | | | 1.524 | 5 | .92 |

The observed values conform very closely with the expected series, though not unreasonably so, and the hypothesis of unit factor inheritance with the ability of taste as the dominant character is therefore substantially upheld.

TABLE X
Sib-pairs available in sibships of 2 and 3 sibs

| Number of Tasters, r | Sib-pairs in Sibships of 2 | Sib-pairs in sibships of 3 in which tasters number | | | | Total, n_{2r} |
|-------------------------------|-------------------------------------|---|----|----|-----|--------------------|
| | | 0 | 1 | 2 | 3 | |
| 0 | 11 | 24 | 8 | .. | .. | 43 |
| 1 | 22 | .. | 16 | 32 | .. | 70 |
| 2 | 74 | .. | .. | 16 | 114 | 204 |
| Total..... | 107 | 24 | 24 | 48 | 114 | 317 |

As an alternative procedure we may take all of the sib-pairs contained in the sibships of 3 and combine the numbers of each

type with those obtained from sibships of 2 only. The sibships of 4 are not used in like manner, since the expected numbers in two classes are less than 5. The 8 trios having no (+) members provide 24 pairs having no (+) members, the 8 trios of 1 (+) member provide 8 pairs of no (+) members and 16 pairs of 1 (+) member, etc. The total contributions of sib-trios to the three sib-pair classes are shown in Table X.

The number of tasters in sib-pairs and trios combined is $170+154=324$, as shown in Table VII, among a total number of individuals, $214+210=424$, giving as the proportion of tasters in sibships of 2 and 3 combined the fraction, $A=324/424$, and the value of p indicated by sibships of both sizes is therefore

$$p = 1 - \sqrt{1 - \frac{324}{424}} = .514357.$$

The expected numbers of sibships having 0, 1, and 2 (+) members are calculated from equations (1), which give

$$\begin{aligned} f_{20} &= 41.2535, \\ f_{21} &= 67.0213, \\ f_{22} &= 208.7252. \end{aligned}$$

Comparing these with the observed values, 43, 70, and 204, χ^2 is found to be 0.313, which for one degree of freedom should be exceeded by chance in about 60 per cent of trials. The data are again in good agreement with the hypothesis of unit factor inheritance with ability to taste as the dominant trait.

To test the hypothesis that the absence of taste (-) is dominant we may test the sib-pair frequencies obtained from sibships of 2 and 3 in a similar manner, as described in the foregoing section. In this case the expected frequencies as calculated from equations (8) turn out to be

$$\begin{aligned} f_{20} &= 45.2394, \\ f_{21} &= 59.0500, \\ f_{22} &= 212.7106, \end{aligned}$$

and χ^2 is 2.499. The deviations are greater than those calculated under the assumption of dominance for taste ability but are not significant in themselves. With one degree of freedom one should expect a χ^2 value of 2.499 to be exceeded by chance in 12 per cent of trials. It thus appears impossible to determine from the data whether tasters or non-tasters are dominant by this method, as might have been expected. Unit factor inheritance of one sort or the other, however, may be confidently assumed.

The hypothesis that ability to taste phenyl-thiocarbamide is determined by non-genetic chance agencies can readily be eliminated. The expected frequencies of sib-pairs containing 0, 1, and 2 tasters under this assumption are, respectively,

$$B^2n_2 = \left(\frac{100}{424}\right)^2 \times 317 = 17.6347,$$

$$2ABn_2 = 2 \times \frac{324}{424} \times \frac{100}{424} \times 317 = 114.2595,$$

and $A^2n_2 = \left(\frac{324}{424}\right)^2 \times 317 = 185.1058.$

Comparing these with the observed numbers, 43, 70, and 204, χ^2 is found to be 55.558, which for one degree of freedom should be exceeded in far less than once in 1000 trials.

SUMMARY

Randomly collected sibships of unspecified parentage may be classified as to their composition and the expected frequency of each sibship type may be calculated from the total number of sibships of each size and from the proportions of the two types of individuals in such sibships. The observed frequencies may then be compared with the expected values by the method of Chi-square. With small numbers of sibships, however, it will usually be impossible to determine which of the two contrasting characters is actually dominant by such a χ^2 -test. If the observed frequencies agree satisfactorily with expectations under an hypothesis of dominance for one character, it may usually be expected that they shall not deviate significantly from expectations under an hypothesis of dominance for the contrasting character. It will usually be possible, however, to eliminate an hypothesis of non-genetic chance determination, if the data are in agreement with the hypothesis of unit factor inheritance.

Applying the χ^2 -test to randomly collected sibships tested for taste deficiency to phenyl-thiocarbamide these generalizations are found to hold true. The data are in excellent agreement with the unit factor hypothesis established by Blakeslee and Salmon and by Snyder.

The Chi-square method should be useful as a check of unit factor inheritance in data which are to be analyzed for autosomal

linkage by the method of Penrose and as a preliminary genetic test in the case of new reaction differences.

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