On the Estimation of the Frequency of Nonpaternity

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SEGREGATION analyses, as well as current methods for the detection of linkage, tacitly assume that all children attributed to a given man and woman, and not clearly at variance genetically with them, are, in fact, their offspring. It can be readily shown, however, that there can exist children who although not the offspring of the man and woman in question are not demonstrably the children of others. The effect of this cryptic nonpaternity or nonmaternity on segregation analyses or linkage studies is difficult to evaluate, but must be related, in some manner, to the over-all frequencies of these events. It is of some importance then to be able to estimate these latter parameters. For a variety of reasons, but primarily because of its presumed greater occurrence, our attention will be directed solely to the estimation of nonpaternity. As we shall use this term, it is *not* synonymous with illegitimacy but rather it encompasses all instances in which the mother of a child incorrectly identifies the child's father. Thus, a child born out of wedlock but as a precondition for marriage would not be included among cases of nonpaternity provided that the mother correctly identified the father of the child.

A relationship exists between the over-all frequency of nonpaternity (λ) and the frequency (D) which can be detected on the basis of examinations of mother, child, and putative father with respect to a particular trait (or group of traits). Under certain conditions, namely, that the biological or "true" father be chosen at random from the population, and that the mother and putative father be unrelated, the ratio, D/λ, can be shown to be a function of gene frequencies alone. With the upsurge in interest in small, primitive communities, many of which have unusual patterns of procreation, it is readily conceivable that two or more of these individuals (mother, "true" father, and putative father) may be related. A more general expression for D/λ, applicable to these situations, is desirable. It is the purpose of this report to derive this more general expression, and to present a method for the estimation of the over-all frequency of nonpaternity. The method also affords estimates of the frequencies of the genes associated with the trait which provides the basis for the paternal exclusion.

THE PROPORTION OF NONPATERNITY WHICH IS DETECTABLE

Intuitively, the proportion of nonpaternity which is detectable must vary with the mode of inheritance of the trait used to demonstrate nonpaternity. Most

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TABLE 1. A SUMMARIZATION OF THE DERIVATION OF A GENERAL EXPRESSION FOR D/λ

Putative father: Genotype σ_p (1)	Putative father: Frequency $P(\sigma_p)$ (2)	"True" father σ_t (3)	$P(\sigma_t\sigma_p)$ (4)	Mother ♀ (5)	$P(♀\sigma_t)$ (6)	Proportion of nonpaternity detectable (7)	Probability of detecting nonpaternity = Σ (2) x (4) x (6) x (7) (8)
AA	p^2	AB	$C_T \cdot q + C_O \cdot 2pq$	AA	$(\frac{1}{2})d_T p + d_O \cdot p^2$	½	$\frac{p^2}{2}(C_T \cdot q + C_O \cdot 2pq)(1 - (\frac{1}{2})d_I - (\frac{1}{4})d_T - d_O \cdot pq)$
				AB	$d_I + (\frac{1}{2})d_T + d_O \cdot 2pq$	¼	
				BB	$(\frac{1}{2})d_T q + d_O \cdot q^2$	½	
		BB	$C_O \cdot q^2$	AA	$d_O \cdot p^2$	1	$p^2(C_O \cdot q^2)(1 - (\frac{1}{2})d_T \cdot p - d_O \cdot pq)$
				AB	$d_T \cdot p + d_O \cdot 2pq$	½	
				BB	$d_I + d_T \cdot q + d_O \cdot q^2$	1	
BB	q^2	AA	$C_O \cdot p^2$	AA	$d_I + d_T \cdot p + d_O \cdot p^2$	1	$q^2(C_O \cdot p^2)(1 - (\frac{1}{2})d_T \cdot q - d_O \cdot pq)$
				AB	$d_T \cdot q + d_O \cdot 2pq$	½	
				BB	$d_O \cdot q^2$	1	
		AB	$C_T \cdot p + C_O \cdot 2pq$	AA	$(\frac{1}{2})d_T \cdot p + d_O \cdot p^2$	½	$\frac{q^2}{2}(C_T p + C_O \cdot 2pq)(1 - (\frac{1}{2})d_I - (\frac{1}{4})d_T - d_O \cdot pq)$
				AB	$d_I + (\frac{1}{2})d_T + d_O \cdot 2pq$	¼	
				BB	$(\frac{1}{2})d_T \cdot q + d_O \cdot q^2$	½	

frequently this trait will be some serotype. Accordingly, we shall be primarily concerned with two genetically different situations. First, we will define the proportion of nonpaternity detectable on the basis of a trait presumed to arise as the consequence of a single pair of autosomal alleles *without* dominance. Second, we will define this proportion when the trait is presumed to arise as a result of a single pair of autosomal alleles *with* dominance. In both instances, we shall assume that the population in question satisfies the Hardy-Weinberg equilibrium conditions, and that the probability, λ, that the "true" father is incorrectly identified is a fixed value independent of genotype or person. Clearly, neither of these assumptions is apt to be precisely fulfilled in any real situation; however, of the two, the constancy of λ would appear to be the more tenuous.

Alleles Without Dominance

Consider, now, the case of two autosomal alleles without dominance, where three genotypes, AA, AB, and BB are distinguishable. Suppose that p is the frequency of the gene A and q ($= 1 - p$) is the frequency of the gene B. Under this system, or for that matter those systems to be considered subsequently, the genetic correlation, ρ, between the putative father and the "true" father can be expressed in terms of three probabilities, c_I, c_T, and c_0, where (see Li and Sacks, 1954)

c_I = probability that the putative and "true" fathers have, at a given locus, two genes identical by descent;

c_T = probability that the putative and "true" fathers have one gene identical by descent;

c_0 = probability that the putative and "true" fathers have no genes identical by descent;

and $c_I + c_T + c_0 = 1$. The corresponding probabilities for the mother and the "true" father are d_I, d_T, and d_0. The specific values to be assigned to these probabilities depend upon the biologic relationship which is postulated; these values are of themselves of no particular moment to our argument.

The derivation of a general expression for D/λ is summarized in table 1. It should be noted that nonpaternity can not be detected if (1) the "true" father is of the same genotype as the putative father, or (2) the putative father is of genotype AB. These cases have, therefore, been omitted from the table. It should also be noted that we have assumed that the "putative" father and mother are unrelated. This is a matter of convenience, and the restriction can be easily removed. Be this as it may, the probability of detecting a case of nonpaternity, D/λ, is equal to the sum of the four elements in column (8). After some manipulation, this expression reduces to

$$\frac{D}{\lambda} = pq\,[1 - (\tfrac{1}{2})\,c_T - c_I]\,[1 - (\tfrac{1}{2})d_I - (\tfrac{1}{4})d_T - d_0pq] + p^2q^2c_0d_I \quad (1)$$

where $[(\frac{1}{2})c_T + c_I]$ is the genetic correlation, ρ, between the putative father and the "true" father, and $[d_I + (\frac{1}{2})d_T]$ is the comparable figure for the mother and "true" father.

Of particular interest are several special situations which can be readily deduced from equation (1). These are the following:

Case 1. If the mother, "true" father, and putative father are all chosen at random, they will have no genes identical by descent. Thus,

$$c_I = d_I = O;\ c_T = d_T = O;\ c_O = d_O = 1;\ \text{and}$$

$$\frac{D}{\lambda} = pq(1 - pq). \tag{2}$$

This expression has been previously given by Wiener (1931), and by Cotterman (1951).

Case 2. If the mother and "true" father are unrelated, but the "true" father is related to the putative father, then

$$d_I = d_T = O;\ d_O = 1;\ \text{and}$$

$$\frac{D}{\lambda} = pq[1 - (\tfrac{1}{2})c_T - c_I]\ (1 - pq)$$

$$\text{or}\ \frac{D}{\lambda} = pq(1 - \rho)\ (1 - pq), \tag{3}$$

where ρ is the correlation between putative and "true" fathers.

Case. 3. If the putative and "true" fathers are unrelated, but the "true" father is related to the mother, then

$$c_I = c_T = O;\ c_O = 1;\ \text{and}$$

$$\frac{D}{\lambda} = pq[1 - (\tfrac{1}{2})d_I - (\tfrac{1}{4})d_T - d_O pq] + p^2q^2d_I. \tag{4}$$

Case 4. Finally, in a population which is completely inbred, all individuals have two genes identical by descent. Therefore

$$c_T = c_O = d_T = d_O = O;\ c_I = d_I = 1;\ \text{and}$$

$$\frac{D}{\lambda} = O.$$

It is moot, of course, whether in this context nonpaternity has any biologic significance.

Alleles with Dominance

We turn now to the case of two alleles with dominance. There are only two recognizable phenotypes, and nonpaternity can be detected only when both the putative father and the mother are of the recessive phenotype, say aa. The general expression, arrived at in a manner analogous to the case of no dominance, is

$$\frac{D}{\lambda} = pq^3[(\tfrac{1}{4})\ c_T d_T + q(c_O d_O + (\tfrac{1}{2})c_T d_O + (\tfrac{1}{2})\ c_O d_T)], \tag{5}$$

where p is the frequency of the gene A, and $q(=1-p)$ is the frequency of the gene a, and c_T, c_O, d_T, and d_O are as previously defined. If the putative and "true" fathers and the mother are unrelated, then

$$c_0 = d_0 = 1;\ c_T = d_T = 0;\ \text{and}$$

$$\frac{D}{\lambda} = pq^4. \tag{6}$$

The arguments here given for a single pair of autosomal alleles can be extended, of course, to multiple autosomal or to sex-linked alleles. To attempt to do so exhaustively, in the former instance, is difficult. As Cotterman (1953) has shown, there are no less than 52 regular three-allele systems, and, since in general, no two have the same statistical properties each requires a separate treatment. On the other hand, an extension of these arguments to sex-linked loci is straightforward. First, we note that all nonpaternity of sons is cryptic; their X-chromosomes are derived from their mothers. Second, and with respect to daughters, to detect nonpaternity the "true" father must be genotypically unlike the putative father. It follows, therefore, that the putative father and "true" father must have no genes identical by descent. The mother and the "true" father may, however, have one gene identical by descent. We find the general expressions to be

$$\frac{D}{\lambda} = pq(1 + q)\,(d_0q + (\tfrac{1}{2})d_T)$$

for the case of sex-linked alleles with dominance (e.g., the human Xg^a system), and

$$\frac{D}{\lambda} = pq[2d_0(1 - pq) + (3/2)d_T]$$

for the case of sex-linked alleles without dominance. In the event, the "true" father and mother are unrelated, these expressions reduce to

$$\frac{D}{\lambda} = pq^2(1 + q)$$

and

$$\frac{D}{\lambda} = 2pq(1 - pq)$$

respectively.

THE ESTIMATION OF λ AND p

To estimate λ and p we proceed as follows: We assume that a series of mother-child-putative father combinations are examined with respect to some trait, and that on the basis of this examination the child, or if you will, the combination, is assigned to one of a series of mutually exclusive categories. The latter recognize the putative father's genotype (or phenotype) and whether the child's genotype (or phenotype) is compatible with that of the putative father. Within a random sample of N combinations, suppose n_i mother-child-putative father groups fall into category *i* (i = 1, 2, ..., k). It is assumed that the n_i are multinomially distributed with parameters N, λ, and p.

TABLE 2. THE DISTRIBUTION OF COMPATIBLE AND INCOMPATIBLE CHILDREN BY GENOTYPE OF PUTATIVE FATHER

PUTATIVE FATHER			CHILD		
			Compatible	Incompatible	Σ
	AA	o	C_1	K_1	
		e	$N[p^2 - \lambda p^2q(1 - pq)]$	$N\lambda p^2q(1 - pq)$	Np^2
	AB	o	C_2	K_2	
		e	$2pqN$	0	$2pqN$
	BB	o	C_3	K_3	
		e	$N[q^2 - \lambda pq^2(1 - pq)]$	$N\lambda pq^2(1 - pq)$	Nq^2
	Σ		$N[1 - \lambda pq(1 - pq)]$	$N\lambda pq(1 - pq)$	N

o = observed number; e = expected number.

Alleles without Dominance

Consider, again, the case of a trait determined by a single pair of autosomal alleles without dominance. There exist six mutually exclusive categories, namely, putative father AA-child compatible (or incompatible); putative father AB-child compatible (or incompatible); putative father BB-child compatible (or incompatible). As previously remarked, one of these cells, putative father AB-child incompatible, is a null set. Table 2 gives expressions for observed and expected numbers of children compatible and incompatible with the genotype of the putative father. It should be noted that the two ways of classification, namely, genotype of putative parent and compatibility of child, are not independent. The partial sums in table 2 can not be multiplied, therefore, to obtain the expected numbers in each cell. We take as the "best" estimates of λ and p those values which maximize the likelihood of the observed array. The likelihood function is

$$L = \frac{N!}{C_1!C_2!C_3!K_1!K_2!K_3!}[p^2 - \lambda p^2q(1 - pq)]^{C_1}[2pq]^{C_2}[q^2 - \lambda pq^2(1 - pq)]^{C_3}[\lambda p^2q(1 - pq)]^{K_1}[\lambda pq^2(1 - pq)]^{K_3}$$

where $N = C_1 + C_2 + C_3 + K_1 + K_2 + K_3$. Differentiation of the logarithm of L with respect to λ and p leads to the expressions

$$\frac{\delta(\log L)}{\delta\lambda}: \frac{K_1 + K_3}{\lambda} - \frac{C_1q(1 - pq)}{1 - \lambda q(1 - pq)} - \frac{C_3p(1 - pq)}{1 - \lambda p(1 - pq)} = 0$$

$$\frac{\delta(\log L)}{\delta p}: \frac{(2C_1 + C_2 + 2K_1 + K_3)}{p} - \frac{(C_2 + 2C_3 + K_1 + 2K_3)}{q} + \frac{(K_1 + K_3)(p - q)}{1 - pq} + \frac{C_1\lambda(1 - 2pq + q^2)}{1 - \lambda q(1 - pq)} - \frac{C_3\lambda(1 - 2pq + p^2)}{1 - \lambda p(1 - pq)} = 0.$$

These equations may be solved iteratively for λ and p.

The variances of the estimates of λ and p may be calculated according to the equations

$$\sigma_\lambda^2 = \frac{I_{pp}}{\Delta};\ \sigma_p^2 = \frac{I_{\lambda\lambda}}{\Delta}$$

where Δ is the determinant of the information matrix,

$$\Delta = \begin{vmatrix} I_{\lambda\lambda} & I_{\lambda p} \\ I_{p\lambda} & I_{pp} \end{vmatrix} = I_{\lambda\lambda}I_{pp} - I_{\lambda p}^2$$

and

$$I_{pp} = \sum_j \frac{1}{e_j}\left(\frac{\delta e_j}{\delta p}\right)^2$$

$$I_{\lambda p} = I_{p\lambda} = \sum_j \frac{1}{e_j}\left(\frac{\delta e_j}{\delta p}\right)\left(\frac{\delta e_j}{\delta \lambda}\right)$$

$$I_{\lambda\lambda} = \sum_j \frac{1}{e_j}\left(\frac{\delta e_j}{\delta \lambda}\right)^2$$

In these expressions, e_j is the expected number in the j^{th} class.

A summary of the calculation of $\left(\frac{\delta e}{\delta \lambda}\right)$ and $\left(\frac{\delta e}{\delta p}\right)$ is presented in table 3.

The algebraic expressions for I_{pp}, $I_{\lambda p}$, and $I_{\lambda\lambda}$ are quite cumbersome, and are, therefore, not presented here. The variances can, of course, be readily calculated by substituting numerical values into the expressions for e, $\frac{\delta e}{\delta \lambda}$, and $\frac{\delta e}{\delta p}$.

Alleles with Dominance

Consider, now, the case of a trait determined by a single pair of autosomal alleles with dominance, say A and a. Again, as a convenience, we assume that the mother, "true" father, and putative father are unrelated. The likelihood function can be shown to be

$$L = \frac{N!}{C_1!C_2!K!}(1 - q^2)^{C_1}(q^2 - \lambda pq^6)^{C_2}(\lambda pq^6)^K$$

where C_1 is the number of children compatible with the dominant phenotype, C_2 the number compatible with the recessive phenotype, and K the number incompatible with the latter phenotype. When the logarithm of this function is differentiated with respect to λ and p, and the resulting equations set equal to zero, we have

$$\frac{2C_1q}{1 - q^2} - \frac{C_2[2 + \lambda q^4(q - 6p)]}{q(1 - \lambda pq^4)} + \frac{K(q - 6p)}{pq} = 0$$

$$\frac{K}{\lambda} - \frac{C_2pq^4}{1 - \lambda pq^4} = 0$$

TABLE 3. THE EXPECTED NUMBERS AND PARTIAL DERIVATIVES APPROPRIATE TO THE VARIOUS PUTATIVE FATHER-CHILD CLASSES

Class		Observed (o)	Expected (e)	$\frac{\delta e}{\delta \lambda}$	$\frac{\delta e}{\delta p}$
Putative father	Child				
AA	Compatible	C_1	$N[p^2 - \lambda p^2 q(1 - pq)]$	$-Np^2q(1 - pq)$	$N[2p - \lambda(2p^3q - 3p^2q^2 + 2pq - p^2)]$
AB	Compatible	C_2	$2Npq$	0	$N[2q - 2p]$
BB	Compatible	C_3	$N[q^2 - \lambda pq^2(1 - pq)]$	$-Npq^2(1 - pq)$	$-N[2q - \lambda(2pq^3 - 3p^2q^2 + 2pq - q^2)]$
AA	Incompatible	K_1	$N\lambda p^2q(1 - pq)$	$Np^2q(1 - pq)$	$N\lambda(2p^3q - 3p^2q^2 + 2pq - p^2)$
AB	Incompatible	K_2	0	0	0
BB	Incompatible	K_3	$N\lambda pq^2(1 - pq)$	$Npq^2(1 - pq)$	$-N\lambda(2pq^3 - 3p^2q^2 + 2pq - q^2)$
Total		N	N	0	0

These equations may be solved directly to obtain

$$q = \sqrt{\frac{C_2 + K}{N}}$$

$$\lambda = \frac{KN^3}{(C_2 + K)^3[N - \sqrt{N(C_2 + K)}\,]}$$

The variances of these estimates can, as before, be obtained from the relationships

$$\sigma^2_\lambda = \frac{I_{pp}}{\Delta};\ \sigma^2_p = \frac{I_{\lambda\lambda}}{\Delta};\ \sigma_{p\lambda} = -\frac{I_{\lambda p}}{\Delta}$$

where, now,

$$I_{\lambda\lambda} = \frac{Npq^6}{\lambda(1 - \lambda pq^4)}$$

$$I_{\lambda p} = \frac{Nq^5\,(q - 4p)}{1 - \lambda pq^4}$$

$$I_{pp} = N\left(\frac{4q^2}{1 - q^2} + \frac{(2 + \lambda q^4(q - 6p)\,)^2}{1 - \lambda pq^4} + \frac{\lambda q^4(q - 6p)^2}{p}\right)$$

Finally, consider the case of a trait determined by a single pair of sex-linked alleles with dominance. For the situation in which the "true" and putative fathers and the mother are unrelated, the likelihood function is

$$L = \frac{N!}{C_1!C_2!K_1!K_2!}\,(q - \lambda pq^3)^{C_1}(p - \lambda pq^2)^{C_2}(\lambda pq^3)^{K_1}(\lambda pq^2)^{K_2}$$

where C_1 and K_1 are the numbers compatible and incompatible with the phenotype (aY), and C_2 and K_2 are the corresponding numbers for the phenotype (AY). If the expressions which are obtained from differentiating log L with respect to λ and p are equated to zero, we have

$$-C_1p(1 + \lambda q^2(q - 3p)\,)\,(1 - \lambda q^2) + C_2q(1 - \lambda q(q - 2p)\,)\,(1 - \lambda pq^2) + (K_1(q - 3p) + K_2\,(q - 2p)\,)\,(1 - \lambda q^2(1 + p) + \lambda^2pq^4) = 0$$

$$\lambda^2Npq^4 - \lambda q^2(\,(K_1 + K_2)\,(1 + p) - (C_1 + C_2 - C_1q)\,) + (K_1 + K_2) = 0$$

where $N = C_1 + C_2 + K_1 + K_2$. These equations may be solved for λ and p by iteration.

The variances of these estimates we obtain from

$$I_{\lambda\lambda} = Npq^2\left(\frac{pq^3}{1 - \lambda pq^2} + \frac{q^2}{1 - \lambda q^2} + \frac{1 + q}{\lambda}\right)$$

$$I_{\lambda p} = \frac{Npq^2[1 - \lambda q^2(3p - q)]}{1 - \lambda pq^2} + \frac{Nq^2[1 + \lambda q(2p - q)]}{1 - \lambda q^2} - Nq^2(3p - q) - Nq(2p - q)$$

$$I_{pp} = \frac{N[1 - \lambda q^2\,(3p - q)]^2}{q(1 - \lambda pq^2)} + \frac{N[1 + \lambda q(2p - q)]^2}{p(1 - \lambda q^2)} + \frac{N\lambda q(3p - q)^2}{p} + \frac{N\lambda(2p - q)^2}{p}$$

TABLE 4. A SUMMARY OF THE CALCULATIONS LEADING TO ESTIMATES OF P AND λ

Class		Observed (o)	Expected (e)	$\frac{\delta e}{\delta \lambda}$	$\frac{\delta e}{\delta p}$	$\frac{1}{e}\left(\frac{\delta e}{\delta \lambda}\right)^2$	$\frac{1}{e}\left(\frac{\delta e}{\delta \lambda}\right)\left(\frac{\delta e}{\delta p}\right)$	$\frac{1}{e}\left(\frac{\delta e}{\delta p}\right)^2$
Putative father	Child							
M	Compatible	59	64.10	−23.87	250.02	8.889	−93.10	9.52
MN	Compatible	129	121.21	0	−24.01	0	0	4.756
N	Compatible	50	52.35	−21.61	−225.31	8.921	93.01	969.7
M	Incompatible	4	2.802	23.87	4.970	203.3	42.34	8.815
MN	Incompatible	0	0	0	0	—	—	—
N	Incompatible	1	2.539	21.61	−5.677	183.9	−48.32	12.69
Σ		243	243.0	0	0	$I_{\lambda\lambda}$ = 405.0	$I_{\lambda p}$ = −6.07	I_{pp} = 1971.

$$\frac{\delta(\log L)}{\delta\lambda} = \frac{5}{.1174} - \frac{59(.4753)(.7506)}{1 - (.1174)(.4753)(.7506)} - \frac{50(.5247)(.7506)}{1 - (.1174)(.5247)(.7506)}$$

$$= -0.02$$

$$\frac{\delta(\log L)}{\delta p} = \frac{256}{.5247} - \frac{235}{.4753} + \frac{5(.0494)}{.7506} + \frac{59(.1174)(1 - .4988 + .2259)}{1 - (.1174)(.4753)(.7506)} - \frac{-50(.1174)(1 - .4988 + .2753)}{1 - (.1174)(.5247)(.7506)}$$

$$= -5.7$$

APPLICATION OF THE METHOD TO A WORKED EXAMPLE

In table 4 are presented unpublished data of Gershowitz on the distribution of M-N blood groups among Detroit Negroes. If p is the frequency of M, and $q = 1 - p$ is the frequency of N, then we take as preliminary estimates of p and q the values obtained by merely counting the M and N genes among the putative fathers, namely,

$$p_1 = \frac{(59 + 4) + (\tfrac{1}{2})(129)}{243} = 0.5247$$

$$q_1 = \frac{(\tfrac{1}{2})(129) + (50 + 1)}{243} = 0.4753$$

The substitution of these values into

$$\frac{\delta \log L}{\delta \lambda} = 0$$

leads to 0.1174 as the preliminary estimate of λ, say λ_1. The estimates p_1, q_1, and λ_1 are used to compute numerical values for $\frac{\delta \log L}{\delta \lambda}$ $(= a)$, $\frac{\delta \log L}{\delta p}$ $(= b)$, $I_{\lambda\lambda}$, $I_{\lambda p}$, and I_{pp}. A summary of these calculations is set out in table 4. The equations

$$I_{\lambda\lambda}\Delta\lambda_1 + I_{\lambda p}\Delta p_1 = a$$
$$I_{\lambda p}\Delta\lambda_1 + I_{pp}\Delta p_1 = b$$

are solved simultaneously for $\Delta\lambda_1$ and Δp_1. Thus

$$405.0\Delta\lambda_1 - 6.07\Delta p_1 = -0.02$$
$$-6.07\Delta\lambda_1 + 1971.\Delta p_1 = -5.7$$

from which

$$\Delta\lambda_1 = -0.00009 \text{ and } \Delta p_1 = -0.0029.$$

New estimates of λ, p, and q are formed according to the equations

$$\lambda_2 = \lambda_1 + \Delta\lambda_1$$
$$p_2 = p_1 + \Delta p_1$$
$$q_2 = 1 - p_2$$

The procedure is repeated until sufficiently small values for $\Delta\lambda$ and Δp are obtained. It is worth noting that this procedure lends itself readily to programming for a digital computer.

In the present instance, after the second iteration, we arrive at the values

$\lambda = 0.1173$ $\quad$ $I_{\lambda\lambda} = 405.6$

$p = 0.5218$ $\quad$ $I_{\lambda p} = -5.41$

$q = 0.4782$ $\quad$ $I_{pp} = 1971.$

Finally, for the variances of λ and p, we obtain

$$\sigma_\lambda = 0.002466$$

$$\sigma_p^2 = 0.000507$$

Thus, the interval defined by the estimate λ plus and minus twice its standard error proves to be 0.018 to 0.217.

The "goodness of fit" of the model to the data is subject to test. If, in the present instance, the observed and expected numbers are contrasted in the conventional x^2 manner, we obtain $x^2 = 2.44$, which for two degrees of freedom is not significant at the 1 per cent level.

SUMMARY

A general expression is derived for the relationship which exists between the over-all frequency of nonpaternity (λ) and the frequency (D) which can be detected on the basis of examinations of mother, child, and putative father with respect to a particular trait. Certain special cases of particular interest are deduced from this more general frequency. A method is then presented for the estimation of the over-all frequency of nonpaternity; the method which is given also affords estimates of the frequencies of the genes associated with the trait which provides the basis for the paternal exclusion.

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