

## AN ENUMERATION OF SOME HUMAN RELATIONSHIPS

BY J. B. S. HALDANE AND S. D. JAYAKAR

*Genetics & Biometry Research Unit, C.S.I.R.*

## INTRODUCTION

In view of the importance attached to relationship in most human cultures, religions, and legal codes, it might be thought that at least the simpler ones, for example those not more distant than that of uncle, would have been enumerated, and a terminology adopted for them, either in colloquial or legal language, or in that of anthropologists. This is not the case. For example if we say that  $B$  is  $A$ 's first cousin we shall show that this may mean any of 48 relationships if the sexes of  $A$  and  $B$  are not specified, and 192 if they are specified. Only a few of these are given special names in any language known to us. All but 6 of the 48 involve at least one multiple marriage, or its biological equivalent, among the grandparents of  $A$  and  $B$ . However even when simultaneous polygamy and divorce are both illegal, remarriage after the death of a spouse is permitted and may be enjoined, and its frequency is shown by the existence of such words as "stepmother" and "half-sister". With increasing study of the extent and effects of human inbreeding an exact terminology is desirable, though we do not suppose that our own cannot be improved. We venture to hope that our enumeration may be of value to anthropologists.

(a) As we are concerned with biological relationships, it is irrelevant whether the parents of any member of the pedigree were married when he or she was born. Nevertheless we shall frequently use the word "marriage" to mean "marriage or its biological equivalent".

(b) We confine ourselves to cognate or "blood" relationships, that is to say relationships between two persons who have at least one known latest common ancestor in common, or of whom one is the ancestor of the other. By "latest common ancestor" is meant the last-born common ancestor. Thus two sons of the same man by different women have two grandparents in common, but their father is their latest common ancestor.

(c) We also confine ourselves to relationships of  $B$  to  $A$  where no latest common ancestor is more remote than a grandparent of  $A$  or  $B$ .

(d) We further neglect the possibility of any inbreeding in the ancestry of  $A$  or  $B$  (though of course their offspring, if any, are inbred). For it can be seen that by condition (c) this would imply a fertile sexual union between parent and offspring or between whole or half brother and sister. A union between grandparent and grandchild, uncle and niece, or aunt and nephew would violate condition (c). Thus if  $A$  is the child of a man and his niece, this means that the same person is  $A$ 's grandparent and great-grandparent. Incestuous unions between parent and offspring, or between sibs, rarely occur, and are still more rarely discovered with certainty. We are aware that in Bali (*vide* Karve, 1953) twins of opposite sex were compelled to marry. A

consideration of such possibilities would greatly extend our analysis. We do however consider unions, such as that of a man with a woman and her daughter by another man, which are forbidden in many cultures. Such unions do not involve inbreeding.

(e) Finally we adopt the convention that the sexes of the relatives  $A$  and  $B$  are irrelevant to the relationship. This convention reduces the number of relationships listed to one quarter of the possible number, and greatly simplifies the symbolism. However it involves some complication in the consideration of sex-linked genes. The structure of most languages is illogical. Thus a man or a woman usually uses the same word for his or her brother, and another for his or her sister, though in India different words of older and younger brothers, and for older and younger sisters, are usual. However a man and a woman almost always use the same words. Thus the description of the relationship of  $B$  to  $A$  depends on the sex of  $B$  and not that of  $A$ . But according to Karve (1953) the Nambudri Brahmins of Kerala are more logical. A woman calls her elder brother "oppa", a man "jyesthan". A woman calls her elder sister "chet-tati" or "jyesthati", a man calls her "oppol". The terms for younger sibs do not appear to depend on  $A$ 's sex.

Ignoring the sexes of  $A$  and  $B$  we have to enumerate 129 distinct relationships, or 516 if the sexes of  $A$  and  $B$  are considered. This large number is mainly due to the possibilities of polygamy, remarriage, and their biological equivalents. If no member of the pedigree has a child by more than one spouse or sexual partner, these numbers are reduced to 17 and 68.

Monozygotic twinning leads to a slight complication. Monozygotic twins have the same genotype apart from mutation, and their children presumably resemble one another as closely as those of the same individual. The effect of such twinning is considered in a special section.

The classification adopted in Roman law (see Morton, 1961 for diagrams) is excellent so far as it goes, and will be adopted here. The degree of consanguinity is the number of "steps" between two relatives, the parent-child relationship being regarded as a step. Thus parents are relatives of degree 1, sibs of degree 2. This system does not take cognizance of half-relationships, and even with the restrictions which we have adopted,  $B$  can be simultaneously related to  $A$  in two different degrees.

A geneticist asks three main types of question about a given relationship:

- (1) What correlations may be expected between the phenotypic characters of  $A$  and  $B$  as the result of their relationship?
- (2) If  $A$  and  $B$  are of different sexes, and have children, how may these children be expected to differ from the general population?
- (3) What are the frequencies in a population studied, of marriages, or their biological equivalent, between relatives of various different kinds, and of progeny of such marriages? These two frequencies are not quite the same if inbreeding affects the net fertility of a marriage, or the viability of its children.

The first two questions can be answered with the aid of coefficients of relationship which are here calculated. It must however be stated that these coefficients may be

misleading for at least five reasons. The population studied may be divided into more or less endogamous groups, based either on geographical isolation, or on religious, occupational, or caste differences. In some societies spouses are positively correlated for certain phenotypic characters, presumably as a result of choice. Selective deaths may alter correlations; thus maternal-foetal incompatibility must raise the correlation between mothers and surviving children with respect to some antigens. There is presumably a tendency for relationships to accumulate. Thus those who are first cousins are probably more often also second or third cousins than are persons unrelated in the fourth degree. Finally the environments of relatives are correlated. All these causes must tend to increase correlations.

All the relationships which we shall consider are irreflexive in the terminology of logic. If  $B$  is  $A$ 's paternal half-brother, he cannot be identical with  $A$ . So we must be careful not to define  $A$ 's paternal half-brother as  $A$ 's father's son, and if we are using symbolic logic, to add the non-identity symbol  $\bar{J}$  where it is needed to ensure irreflexivity (see Carnap, 1958, pp. 117, 223). None of the relations in our list is transitive, like "ancestor" and "descendant". Some are intransitive, others non-transitive, for example the relation "whole sib". The symmetry or otherwise of relationships is more important. It is clear that some relationships are symmetric, for example if  $B$  is  $A$ 's mother's whole sister's child,  $A$  is  $B$ 's mother's whole sister's child. Others are asymmetric. Thus if  $B$  is  $A$ 's mother's whole brother's child,  $A$  is  $B$ 's father's whole sister's child. Such asymmetric relations evidently occur in pairs, each member of a pair being the converse of the other. A third class of relations, the non-symmetric, also exists. If  $B$  has a relation  $R$  of this class to  $A$ , then  $A$  may or may not have it to  $B$ . Thus if  $B$  is  $A$ 's sister,  $A$  may be  $B$ 's sister or her brother. None of the relations in our classification fall into this class, as they would do if  $B$ 's sex were specified while  $A$ 's was not. We avoid this class either by specifying the sex of neither  $A$  nor  $B$ , or by specifying the sex of both. We can thus classify all our 129 relationships as symmetrical or fully asymmetrical. In fact 37 are symmetrical, and the other 92 occur in converse pairs.

#### COEFFICIENTS OF RELATIONSHIP

The terminology of coefficients of relationship is unfortunately imprecise. Wright (1922) used the lower case letter  $f$  for his coefficient, which is much the most important of the group. Recent authors have however used  $F$ . Haldane and Moshinsky (1939) used  $f'$  for sex-linked loci. This had however been used by Wright for  $f_{n-1}$  when  $f$  denoted  $f_n$ . We suggest that the Greek letter  $\phi$  be used.  $f$  and  $\phi$  enable us to make statements about the gametes of  $B$ , given information about a gamete of  $A$ . But we also require information about the diploid genotype of  $B$ , given that of  $A$ . This information may be given by two more coefficients,  $F$  for autosomal loci, and  $\Phi$  for sex-linked loci in members of the homogametic sex. A similar coefficient for  $Y$ -linked genes would be unity for males with a latest common male ancestor connected to each by a series of males, (e.g. if  $B$  is  $A$ 's father's paternal half-brother) and otherwise zero.

The values of  $f$  and  $F$  are independent of the sexes of  $A$  and  $B$ , so no difficulty arises from grouping our relations in fours. But this is not so for  $\phi$ , which may be defined as the limiting probability, when a sex-linked gene is very rare, that if it is present in a gamete of  $A$ , it will also be found in the first gamete of  $B$  examined. This probability differs with the sexes of  $A$  and  $B$  and may assume four different values. By listing these, we have been able to reduce our list of relationships from 516 to 83, and we consider that this compensates for a possible lack of logicity. Our definitions, which follow, are based on Malécot's (1948) useful fiction of an ancestral population in which any given allele was present at only one locus. This greatly facilitates the calculation of the coefficients in finite pedigrees. We shall call such a gene 'rare'. From these definitions one can readily calculate probabilities when a gene is not rare.

$f$  symbolizes Wright's coefficient of relationship or of inbreeding. It is more precisely described as the coefficient of single autosomal relationship. The rules for its calculation are well-known.  $f_{AB} = f_{BA}$  is the probability that if  $A$  has produced a gamete carrying a rare gene, the first tested gamete of  $B$  will carry the same gene. When the gene has a frequency  $q$  in the population this probability becomes  $q + f(1 - q)$ . If there is no dominance, the somatic resemblance between  $A$  and  $B$  for any character is given by the correlation

$$\begin{aligned} \rho_{AB} &= \frac{2\sigma^2 f_{AB}}{\sigma^2 + \epsilon^2} \\ &= 2h^2 f_{AB}. \end{aligned}$$

where  $\sigma^2$  is the part of the variance of the character concerned due to additive gene effects,  $\epsilon^2$  the part due to inhomogeneity of the environment, and  $h^2$  its heritability. (Here and later we neglect maternal effects, environmental correlation between relatives, epistasis, and other complicating factors listed by Lerner (1950), Kempthorne (1957) and others.) However dominance introduces a complication. If  $A$  and  $B$  are related through both parents of each, then there is a finite probability  $F_{AB}$ , when neither  $A$  nor  $B$  is inbred (i.e.  $f_A = f_B = 0$ ) that if  $A$  is homozygous for a rare gene,  $B$  will also be homozygous. This, as Malécot showed, can be calculated as follows. If  $P$  and  $Q$  are the parents of  $A$ ,  $R$  and  $S$  those of  $B$ , then

$$\begin{aligned} F_{AB} &= f_{PR} f_{QS} + f_{PS} f_{QR}, \\ \text{while } f_{AB} &= \frac{1}{4}(f_{PR} + f_{QS} + f_{PS} + f_{QR}). \end{aligned}$$

If now  $F_{AB}$  is not zero, their somatic resemblance is given by

$$\rho_{AB} = \frac{2\sigma^2 f_{AB} + \tau^2 F_{AB}}{\sigma^2 + \tau^2 + \epsilon^2}$$

where  $\tau^2$  is the part of the variance of the character concerned due to "dominance deviations",

Fisher (1918) first explained the higher correlations between sibs than between parent and offspring on these lines.  $\bar{F}$  is usually zero, for example for ordinary first cousins, but it is not zero for double half first cousins, though a large sample would be needed to verify the increased correlation. If  $p + q = 1$ , the array of  $B$ , given that  $A$  is **gg**, and **G** stands for any allelomorph of **g**, is

$$(1 - 4f + F)p^2 \mathbf{GG} + 2p[q + 2f(p - q) - Fp] \mathbf{Gg} + (q^2 + 4fpq + Fp^2) \mathbf{gg}.$$

The value of  $F_{AB}$  is irrelevant to the offspring of  $A$  and  $B$ .

$\phi_{AB}$  is similarly definable as the probability that if  $A$  has produced a gamete carrying a rare sex-linked gene, the first tested gamete of  $B$  will carry the same gene.  $\phi$  is defined as their coefficient of single sex-linked relationship; and it is easily seen that  $\phi_{BA} = \phi_{AB}$ . If  $A$  and  $B$  have a child  $C$ ,  $\phi_C$  is not defined if  $C$  is a male. If  $C$  is a female  $\phi_C = \phi_{AB}$  is her coefficient of sex-linked inbreeding. When the gene  $s$  is not rare but has a frequency  $q$ , and  $p+q=1$ , then the probable genotypes of  $B$ , if  $A$  has produced a gamete carrying  $s$ , are:—

$$\begin{aligned} \text{♂ } & (1-f)p\mathbf{S} + (q+fp)\mathbf{s} \\ \text{♀ } & (1-2f)p^2\mathbf{SS} + 2(pq+fp^2-fpq)\mathbf{Ss} + (q^2+2fpq)\mathbf{ss} \end{aligned}$$

where  $\mathbf{S}$  stands for all alleles of  $s$ .

Haldane and Moshinsky (1939) gave rules for calculating  $\phi_{AB}$  which are correct if none of their latest common ancestors are inbred, as in the pedigrees here considered. The amended rules, valid for a finite pedigree, are as follows. List all paths by which  $A$  and  $B$  are connected to latest common ancestors. Ignore any path passing through two males in succession. Count the steps in the remainder with the following conventions. The step from mother to daughter counts as one. That from father to daughter counts as zero, so does that from mother to son, except that where a woman is a latest common ancestor the steps between two of her sons count as one. If  $n_i$  is the number of steps so counted in the  $i$ -th path from  $A$  to  $B$ , and  $\phi_i$  is the coefficient of sex-linked inbreeding of the latest common ancestor (if a woman) on this path, then

$$\phi_{AB} = \sum 2^{-n_i} - 1(1 + \phi_i).$$

Similarly if  $P$  and  $Q$  are the parents of  $A$ ,  $R$  and  $S$  those of  $B$ ,

$$\Phi_{AB} = \phi_{PR}\phi_{QS} + \phi_{PS}\phi_{QR},$$

with the further convention that if  $P \equiv R$ ,  $\phi_{PR} = 1$  if  $P$  is a male, and  $\phi_{PR} = \frac{1}{2}$  if  $P$  is a female. This is the probability that if  $A$  is  $\mathbf{ss}$ ,  $B$  will also be  $\mathbf{ss}$ . In practice it is simpler to calculate these values directly, adopting Malécot's fiction, for the 18 fundamental relationships from which all the others in Table 1 except  $F$  and  $\Phi$  can be built up by addition.

#### THE LOGICAL STRUCTURE OF HUMAN RELATIONSHIPS

Carnap (1958) describes human relationships in terms of symbolic logic in his sections 15c, 17b, 30c, 31b, 54a, 54b, and 55c. He is able to derive all cognate relationships from the relation *Par* (Parent of) and the class *Mi* (Male), though in this system  $x$  is only said to be the husband of  $y$  if he has begotten a child by her. Further primitive signs are needed for legal relationships such as "Husband of", but they do not concern us here. Logicians have been more interested in defining relationships for which names already exist than in enumeration. In practice we gain in symmetry by adopting two primitive signs  $M$  and  $P$  for relations, rather than one. Let  $M$  designate the maternal relationship, i.e.  $M(x, y)$  means "x is the mother of y", and let  $P$  similarly designate the paternal relationship. Instead of  $M^{-1}$  and  $P^{-1}$  for the converse relationships we shall use Russell's (1903) sign  $\tilde{M}$  and  $\tilde{P}$ .  $\tilde{M}(x, y)$  means that  $x$  is a child born of  $y$ , or  $y$  the mother of  $x$ .  $M$  and  $P$  are one-valued,  $\tilde{M}$  and  $\tilde{P}$  are many-valued.

The logical products of all these four symbols are null for the human species. Thus  $M.P$  would mean that  $x$  was both mother and father of  $y$ , which is only possible in self-fertilized organisms. However their relative products are meaningful. Thus  $M|M$  means maternal grandmother, and  $M|P$  paternal grandmother (mother of father). Cognate relationships involving a common ancestor are symbolized by a series of one or more inverse signs followed by one or more direct signs. The first direct sign must be the converse of the last converse sign. Thus  $M|P$  is null. It means that  $x$ 's mother is  $y$ 's father.  $M|M$  means that  $x$  and  $y$  have the same mother. To ensure that  $x$  is not identical with  $y$  we must use the non-identity sign  $\mathcal{J}$ . Thus  $\tilde{M}|M.\mathcal{J}$  means that  $x$  has the same mother as  $y$  but is not identical.  $x$  and  $y$  often have several latest common ancestors. Thus  $M|M.\tilde{P}|P.\mathcal{J}$  means that  $x$  has the same mother as  $y$ , and also the same father, and is not identical; hence  $x$  is  $y$ 's whole-sister or brother. This is however a somewhat cumbrous expression, which we replace by a single letter. However we are aware that logicians may prefer a symbolism which fits into the corpus of symbolic logic. And it may also readily be translated into the symbols of binary arithmetic. Thus if  $x$  is the child of  $y$ 's mother's father and of  $y$ 's father's whole sister, a relation which we symbolize by  $\left. \begin{matrix} wH \\ hMw \end{matrix} \right\}$ , the relationship in the terminology of this section is  $(\tilde{P}|P.\mathcal{J})|M.\tilde{M}|(\tilde{M}|M.\tilde{P}|P.\mathcal{J})|P$ . If we write  $\theta$  for  $\tilde{M}$  and  $M$  and  $1$  for  $\tilde{P}$  and  $P$ , using a decimal point for the latest common ancestor, with the convention that children of the same parent are not identical, this becomes  $1\cdot10\cdot00\cdot01\cdot01\cdot11$ , using Russell's sign for logical product. It is instructive to note why we could not use symbols for "Son of" and "Daughter of" as our primitive signs.

#### SYMBOLISM

In the interests of brevity we use the following symbolism. Each letter stands for a human being.  $w$  means a wife, woman, Weib, etc.  $h$  means a man (husband, homme, Herr, homo, etc.). The symbols  $m$  (which may mean male, man, maschio, mother, Mutter, mā (Hindi) etc.) and  $f$  (which may mean father, female, femme, etc.) are liable to be misleading. Any set of letters (not more than three in this paper) symbolises a relationship of  $B$  to  $A$  through a common ancestor, beginning with  $A$ 's parent. The common ancestor is written with a capital letter; and letters subsequent to it represent descendants of the common ancestor, and ancestors of  $B$ . Thus  $wH$  means that  $A$ 's mother  $w$  was a daughter of  $H$ , the father of  $B$ . Thus  $B$  is  $A$ 's maternal half-uncle. Similarly  $hWh$  means that  $B$  is the child of  $A$ 's maternal half-brother. If there are several common ancestors we use a bracket. Thus  $\left. \begin{matrix} hH \\ wWw \end{matrix} \right\}$  means that  $A$ 's paternal grandfather  $H$  had a child  $B$  by the maternal half sister of  $A$ 's mother. That is to say  $H$  married his son's wife's maternal half-sister. Thus both  $H$  and  $W$  must have married twice (or had children by two sexual partners). Where a pair of common ancestors are married, we use the symbol  $M$ . Thus  $hM$  replaces  $\left. \begin{matrix} hW \\ hH \end{matrix} \right\}$  and means that  $B$  is a whole sib of  $A$ 's father  $h$ , that is to say a paternal aunt or uncle of  $A$ .

We are aware that we have no symbols for the relationships in a direct ancestral line, namely parent and child, and the symbols are ambiguous for grandparent, and grandchild, which come within our scope. But here unambiguous words or phrases are available in most languages. The Indian languages are richer than the European in terms for relationships. Thus in Hindi "brother" is "bhai" and "sister" "bahin" or "bahān". The four types of male first cousin, namely the sons of *A*'s mother's sister, mother's brother, father's sister, and father's brother (in our symbolism *wMw*, *wMh*, *hMw*, and *hMh*) are called *mausera-bhai*, *mamera-bhai*, *phuphera-bhai*, and *chachera-bhai*, respectively, their sisters being called *mauseri-bahan*, etc. These are derived from the names of the four types of aunt and uncle. But although remarriage of widowers is normal in northern India, and polygyny was not rare, there are no special words for *wHw*, etc. There is therefore a need for a symbolism.

In translating our symbolism into that of symbolic logic, the order should be reversed. *w* before the capital becomes  $\bar{M}$ , after it *M*. *h* before the capital becomes  $\bar{P}$ , after it *P*. *W* becomes  $\bar{M}|M$ .  $\bar{J}$ ; *H* becomes  $\bar{P}|P$ .  $\bar{J}$ , and *M* becomes  $(\bar{M}|M. \bar{P}|P. \bar{J})$ . Inclusion in a bracket is replaced by the full stop or other sign for a logical product or intersection class.

### THE ENUMERATION

Table 1 gives our enumeration. The third column gives the converse of each relationship. *S* denotes that a relationship is symmetrical, and is therefore its own converse. There are only 17 relationships which do not involve at least one remarriage. They are the six relations between ancestor and descendant which head our list, and the following:—

$M, wM, Mw, hM, Mh, wMw, wMh, hMw, hMh, \left. \begin{matrix} wMw \\ hMh \end{matrix} \right\},$  and  $\left. \begin{matrix} wMh \\ hMw \end{matrix} \right\}$ . In Indian communities where widows do not remarry, relationships containing the letter *W* do not occur, or are not recognized.

Some of the multiple relationships involving remarriage or polygamy are no doubt bizarre, and several of them can only occur after marriages to agnates (spouse's blood-relatives) which are forbidden in some cultures. However they are often encouraged in others. Thus where a man marries two full sisters, simultaneously or successively, their children will be in the relation  $\left. \begin{matrix} H \\ wMw \end{matrix} \right\}$  (paternal half sib and full cousin) to one another. Again in some polygamous cultures, and particularly in ruling families, a man might inherit his father's wives and concubines, and have access to all of them but his own mother. The child of a woman by her first husband and by his son by another wife are in the relationship  $\left. \begin{matrix} W \\ Hh \end{matrix} \right\}$ , that is to say *B* is *A*'s maternal half-brother and paternal nephew. Mythology furnishes examples of still stranger relationships. Thus in the Mahabharata the children of the brothers Yudhiṣṭhira and Arjuna by their co-wife Draupadi were legally  $\left. \begin{matrix} W \\ hMh \end{matrix} \right\}$ ; but since according to the epic Yudhiṣṭhira

Table 1. Relationships and coefficients of relationship

	Relation	Symbol	Converse	$f$	$F$	$\phi_{11}$	$\phi_{12}$	$\phi_{21}$	$\phi_{22}$	$\Phi$
1, 2	Degree 1 Parent	—	Child	$\frac{1}{4}$	0	0	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{4}$	0
1, 2	Degree 2 Mother's Parent	—	Daughter's child	$\frac{1}{8}$	0	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	0
3, 4	Father's Parent	—	Son's child	"	"	0	0	0	$\frac{1}{8}$	0
5	Maternal half sib	$W$	$S$	$\frac{1}{8}$	0	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	0
6	Paternal half sib	$H$	$S$	"	"	0	0	0	$\frac{1}{8}$	0
7	Full sib	$M$	$S$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$
1, 2	Degree 3 Half aunt or uncle	$wW$	$Ww$	$\frac{1}{8}$	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	0
3, 4	" " "	$wH$	$Hw$	"	"	0	0	0	$\frac{1}{8}$	"
5, 6	" " "	$hW$	$Wh$	"	"	0	0	0	$\frac{1}{8}$	"
7, 8	" " "	$hH$	$Hh$	"	"	0	0	0	$\frac{1}{8}$	"
9, 10	Aunt or uncle	$wM$	$Mw$	$\frac{1}{8}$	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	0
11, 12	" " "	$hM$	$Mh$	"	"	0	0	0	$\frac{1}{8}$	0
13, 14	Double half aunt or uncle (Fig. 1)	$wW$ $hH$ }	$Ww$ $Hh$ }	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	0
15, 16	" " "	$wH$ $hW$ }	$Hw$ $Wh$ }	"	"	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
17, 18	Half aunt or uncle and half niece or nephew (Fig. 2)	$wW$ $hH$ }	$Ww$ $hH$ }	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	0
19	" " "	$wH$ $hW$ }	$S$	"	"	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
20	" " "	$hW$ $Wh$ }	$S$	"	"	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
I	Degree 4 One common grand- parent									
1	Half first cousin Fig. 3	$wWw$	$S$	$\frac{1}{8}$	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	0
2	" " "	$wHw$	$S$	"	"	0	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	"
3, 4	" " "	$wWh$	$hWw$	"	"	0	0	0	$\frac{1}{8}$	"
5, 6	" " "	$wHh$	$hHw$	"	"	0	0	0	$\frac{1}{8}$	"
7	" " "	$hWh$	$S$	"	"	0	0	0	$\frac{1}{8}$	"
8	" " "	$hHh$	$S$	"	"	0	0	0	$\frac{1}{8}$	"
II	Two common grand- parents									
A	No remarriage									
9	Full first cousin (Fig. 4)	$wMw$	$S$	$\frac{1}{8}$	0	$\frac{3}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{3}{8}$	0
10, 11	" " "	$wMh$	$hMw$	"	"	0	$\frac{1}{8}$	0	$\frac{1}{8}$	"
12	" " "	$hMh$	$S$	"	"	0	0	0	$\frac{1}{8}$	"
B	Two-remarriages									
13	Double half first cousin (Fig. 5)	$wWw$ $hWh$ }	$S$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{5}{8}$	$\frac{1}{8}$
14	" " " "	$wWw$ $hHh$ }	$S$	"	"	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{3}{8}$	0
15	" " " "	$wHw$ $hWh$ }	$S$	"	"	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{3}{8}$	$\frac{1}{8}$



Table 1. Relationships and coefficients of relationship—(Contd.)

	Relation	Symbol	Converse	$f$	$F$	$\phi_{11}$	$\phi_{12}$	$\phi_{21}$	$\phi_{22}$	$\Phi$
B	Two remarriages									
16	Double half first cousin	$wHw$ $hHh$	$S$	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	0
17	" " " "	$wWh$ $hWw$	$S$	"	"	0	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$
18	" " " "	$wHh$ $hHw$	$S$	"	"	0	0	0	0	0
19, 20	" " " "	$wHw$ $hWw$	$wHh$ $hWw$	"	"	0	$\frac{1}{8}$	0	$\frac{1}{16}$	0
C	Double remarriage									
21, 22	Double half first cousin (Fig. 6)	$wWw$ $wHh$	$wWw$ $hHw$	$\frac{1}{16}$	0	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{1}{16}$	0
23, 24	" " " "	$wWh$ $wHw$	$wHw$ $hWw$	"	"	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	0
25, 26	" " " "	$wWh$ $hHh$	$hWw$ $hHh$	"	"	0	$\frac{1}{8}$	0	$\frac{1}{16}$	0
27, 28	" " " "	$wHh$ $hWh$	$hHw$ $hWh$	"	"	0	0	0	$\frac{1}{8}$	0
III	Three common grandparents									
A	One remarriage									
29	Full and half first cousin (Fig. 7)	$wMw$ $hWh$	$S$	$\frac{3}{32}$	$\frac{1}{16}$	$\frac{3}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{7}{32}$	$\frac{1}{16}$
30	" " " "	$wMw$ $hHh$	$S$	"	"	$\frac{3}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{3}{32}$	0
31, 32	" " " "	$wMh$ $wWh$	$hMw$ $wWh$	"	"	0	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	0
33, 34	" " " "	$wMh$ $hHh$	$hMw$ $wHh$	"	"	0	$\frac{1}{8}$	0	$\frac{1}{16}$	0
35	" " " "	$hMh$ $wWw$	$S$	"	"	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{5}{32}$	$\frac{1}{16}$
36	" " " "	$hMh$ $wHw$	$S$	"	"	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{8}$
B	Triple remarriage									
37	Triple half first cousin (Fig. 8)	$wWh$ $hWw$ $wHw$	$S$	$\frac{3}{32}$	$\frac{1}{16}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{16}$	$\frac{1}{16}$
38, 39	" " " "	$wWw$ $wHh$ $hWh$	$wWw$ $hHw$ $hWh$	"	"	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{5}{32}$	$\frac{1}{16}$
40	" " " "	$wWw$ $wHh$ $hHw$	$S$	"	"	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{1}{16}$	0
41	" " " "	$wWh$ $hHh$ $hWw$	$S$	"	"	0	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$
42, 43	" " " "	$wHw$ $wWh$ $hHh$	$wHw$ $hWw$ $hHh$	"	"	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	0
44	" " " "	$wHh$ $hHw$ $hWh$	$S$	"	"	0	0	0	$\frac{1}{8}$	0

Table 1. Relationships and coefficients of relationship—(Contd.).

	Relation	Symbol	Converse	$f$	$F$	$\phi_{11}$	$\phi_{12}$	$\phi_{21}$	$\phi_{22}$	$\Phi$
IV	Four common grandparents									
A	Two marriages									
45	Double first cousin (Fig. 9)	$wMw$ $hMh$	$S$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{3}{8}$	$\frac{3}{16}$	$\frac{3}{16}$	$\frac{7}{32}$	$\frac{3}{16}$
46	" " "	$wMh$ $hMw$	$S$	"	"	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$
B	Cyclical remarriage									
47	Quadruple half first cousin (Fig. 10)	$wWw$ $wHh$ $hWh$ $hHw$	$S$	"	$\frac{3}{32}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{5}{32}$	$\frac{1}{16}$
48	" " "	$wWh$ $wHw$ $hWw$ $hHh$	$S$	"	"	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{3}{16}$	$\frac{1}{16}$
1, 2	Degrees 2 and 3 Half sib and half aunt or uncle (Fig. 11)	$W$ $hH$	$W$ $Hh$	$\frac{3}{16}$	$\frac{1}{8}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	0
3, 4	" " "	$H$ $wW$	$H$ $Ww$	"	"	$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{5}{16}$	$\frac{1}{4}$
I	Degrees 2 and 4 Two remarriages				0					
1	Half sib and half first cousin (Fig. 12)	$W$ $hWh$	$S$	$\frac{3}{32}$	$\frac{1}{16}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
2	" " "	$W$ $hHh$	$S$	"	"	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	0
3	" " "	$H$ $wWw$	$S$	"	"	$\frac{1}{2}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{3}{32}$	$\frac{1}{8}$
4	" " "	$H$ $wHw$	$S$	"	"	$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{4}$
II	One remarriage									
5	Half sib and full cousin (Fig. 13)	$W$ $hMh$	$S$	$\frac{3}{16}$	$\frac{1}{8}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
6	" " "	$H$ $wMw$	$S$	"	"	$\frac{3}{8}$	$\frac{3}{16}$	$\frac{3}{16}$	$\frac{3}{16}$	$\frac{3}{8}$
I A	Degrees 3 and 4 One remarriage									
1, 2	Half aunt or uncle and half cousin (Fig. 14)	$wW$ $wHh$	$Ww$ $hHw$	$\frac{3}{32}$	0	$\frac{1}{2}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	0
3, 4	" " "	$wH$ $wWw$	$Hw$ $wWw$	"	"	$\frac{1}{8}$	$\frac{5}{16}$	$\frac{1}{16}$	$\frac{5}{32}$	0
5, 6	" " "	$hW$ $hHh$	$Wh$ $hHh$	"	"	0	0	$\frac{1}{2}$	$\frac{1}{8}$	0
7, 8	" " "	$hH$ $hWw$	$Hh$ $wWh$	"	"	0	0	$\frac{1}{8}$	$\frac{1}{16}$	0

Table 1. Relationships and coefficients of relationship—(Contd.)

	Relation	Symbol	Converse	$f$	$F$	$\phi_{11}$	$\phi_{12}$	$\phi_{21}$	$\phi_{22}$	$\Phi$
B	Two remarriages									
9, 10	Half aunt or uncle and half cousin (Fig. 15)	$wW$ $hWh$	$Ww$ $hWh$	$\frac{1}{32}$	$\frac{1}{32}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{3}{16}$	$\frac{1}{8}$
11, 12	" " "	$wW$ $hHh$	$Ww$ $hHh$	"	"	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	0
13, 14	" " "	$wH$ $hWw$	$Hw$ $wWh$	"	"	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{3}{16}$	$\frac{1}{8}$
15, 16	" " "	$wH$ $hWw$	$Hw$ $wHh$	"	"	0	$\frac{1}{4}$	0	$\frac{1}{8}$	0
17, 18	" " "	$hW$ $wWh$	$Wh$ $hWw$	"	"	0	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{3}{16}$	$\frac{1}{8}$
19, 20	" " "	$hW$ $wHh$	$Wh$ $hHw$	"	"	0	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	0
21, 22	" " "	$hH$ $wWw$	$Hh$ $wWw$	"	"	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{1}{32}$	0
23, 24	" " "	$hH$ $wHw$	$Hh$ $wHw$	"	"	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	0
II A	Double remarriage									
25, 26	Half aunt or uncle and double half cousin (Fig. 16)	$wW$ $wHh$ $hWh$	$Ww$ $hHw$ $hWh$	$\frac{1}{8}$	$\frac{1}{32}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{3}{16}$	$\frac{1}{8}$
27, 28	" " "	$wH$ $wWw$ $hHw$	$Hw$ $wWw$ $wHh$	"	"	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{3}{32}$	0
29, 30	" " "	$hW$ $hHh$ $wWh$	$Wh$ $hHh$ $hWw$	"	"	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{3}{16}$	$\frac{1}{4}$
31, 32	" " "	$hH$ $hWw$ $wHw$	$Hh$ $wWh$ $wHw$	"	"	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	0
II B	One remarriage									
33, 34	Half aunt or uncle and cousin (Fig. 17)	$wW$ $hMh$	$Ww$ $hMh$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{8}$
35, 36	" " "	$wH$ $hMw$	$Hw$ $wMh$	"	"	0	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{3}{16}$	$\frac{1}{8}$
37, 38	" " "	$hW$ $wMh$	$Wh$ $hMw$	"	"	0	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{3}{16}$	$\frac{1}{8}$
39, 40	" " "	$hH$ $wMw$	$Hh$ $wMw$	"	"	$\frac{3}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{3}{32}$	0
III	Two remarriages									
41	Half aunt or uncle, half nephew or niece, and half cousin (Fig. 18)	$wH$ $Hw$ $wWw$	$S$	$\frac{5}{32}$	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{5}{16}$	$\frac{5}{16}$	$\frac{9}{32}$	$\frac{1}{4}$
42	" " "	$hW$ $Wh$ $hHh$	$S$	"	"	0	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$

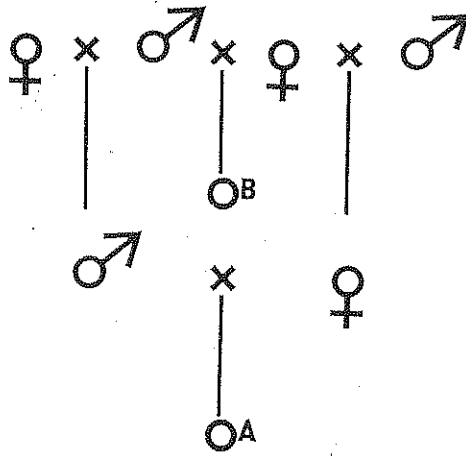


Fig. 1 The relationship symbolised by  $\begin{Bmatrix} wW \\ hH \end{Bmatrix}$

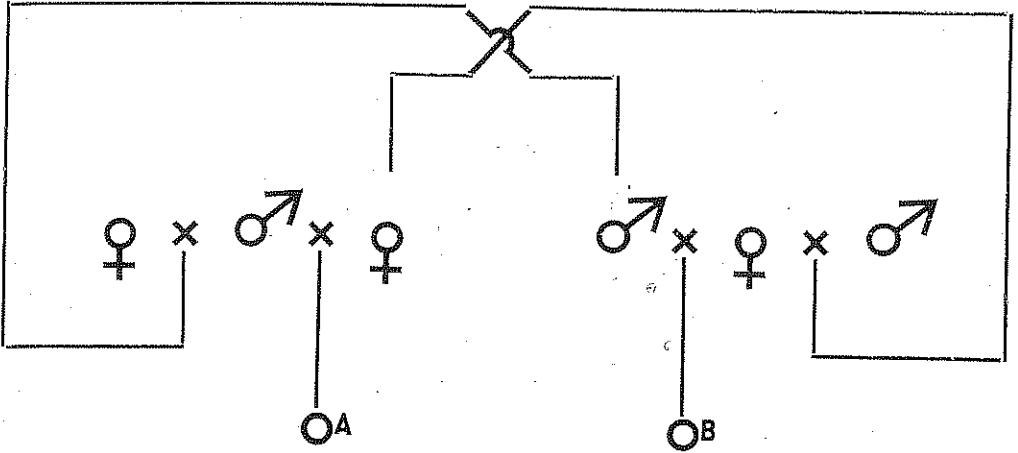


Fig. 2 The relationship symbolised by  $\begin{Bmatrix} wW \\ Hh \end{Bmatrix}$

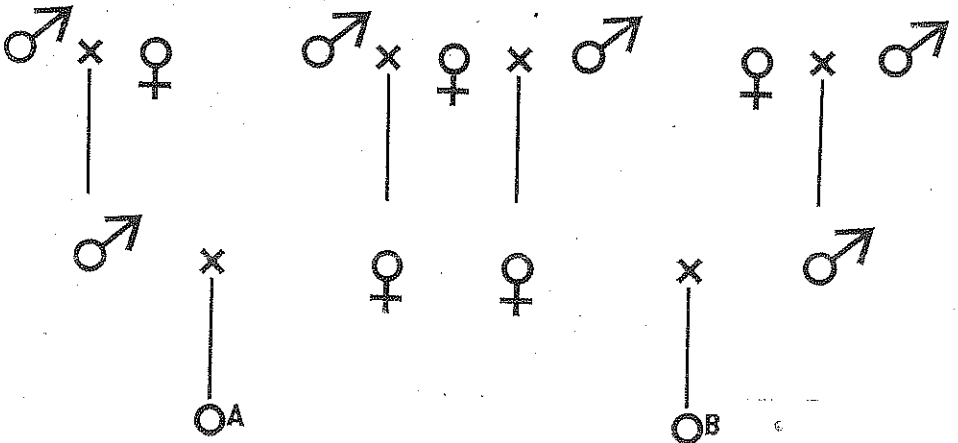


Fig. 3 The relationship symbolised by  $wWw$

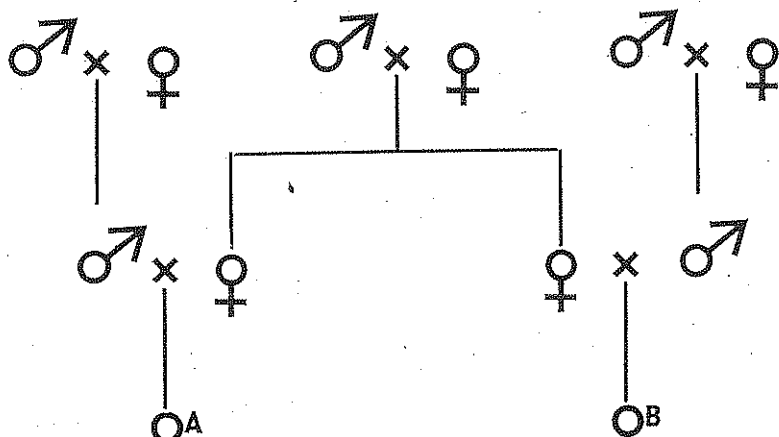


Fig. 4 The relationship symbolised by  $wMw$

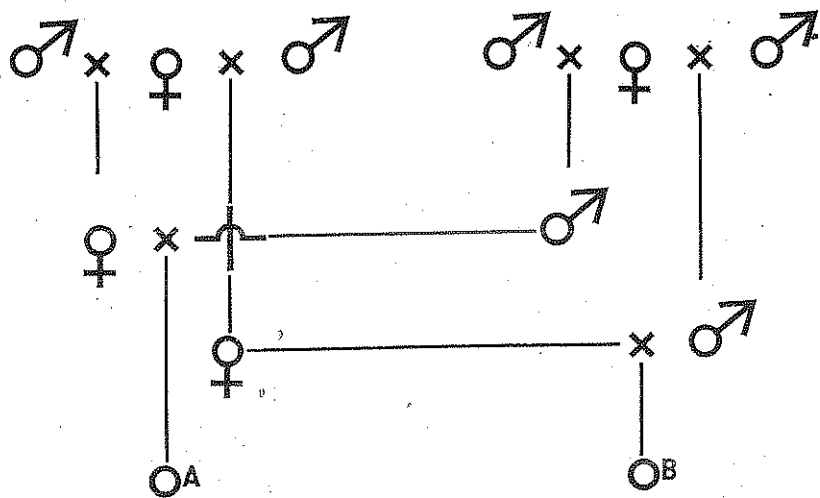


Fig. 5 The relationship symbolised by  $\begin{cases} wWw \\ hWh \end{cases}$

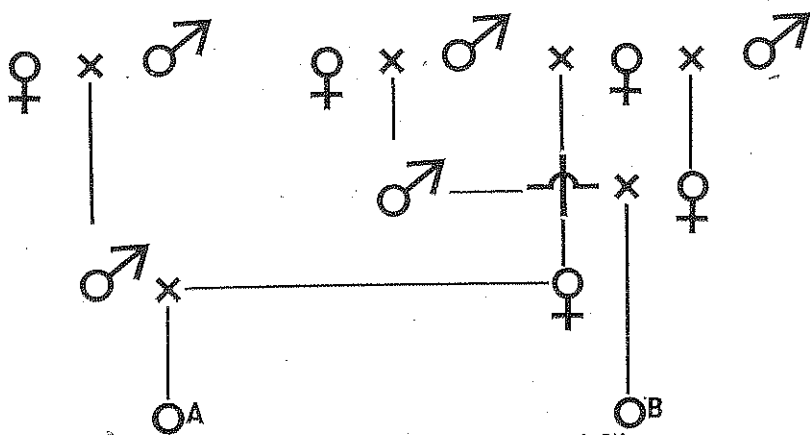


Fig. 6 The relationship symbolised by  $\begin{cases} wWw \\ wHh \end{cases}$

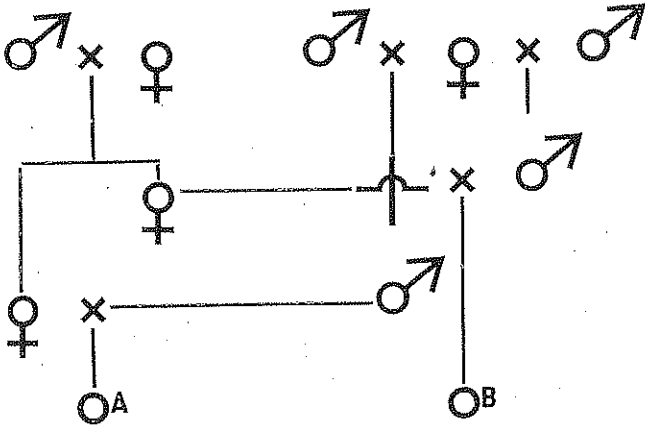


Fig. 7 The relationship symbolised by  $\begin{Bmatrix} wMw \\ hWh \end{Bmatrix}$

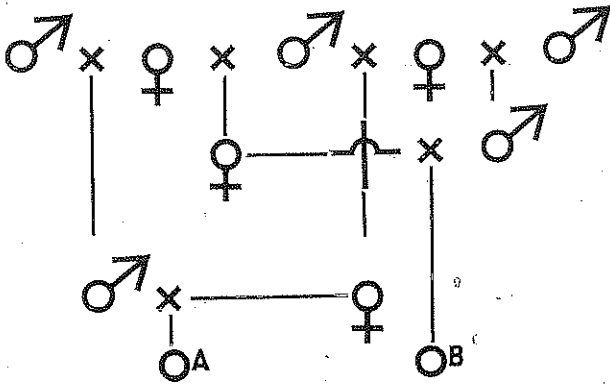


Fig. 8 The relationship symbolised by  $\begin{Bmatrix} wWw \\ hWh \\ wHw \end{Bmatrix}$

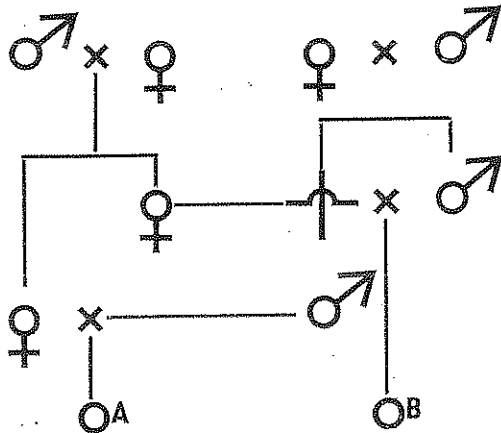


Fig. 9 The relationship symbolised by  $\begin{Bmatrix} wMw \\ hMh \end{Bmatrix}$

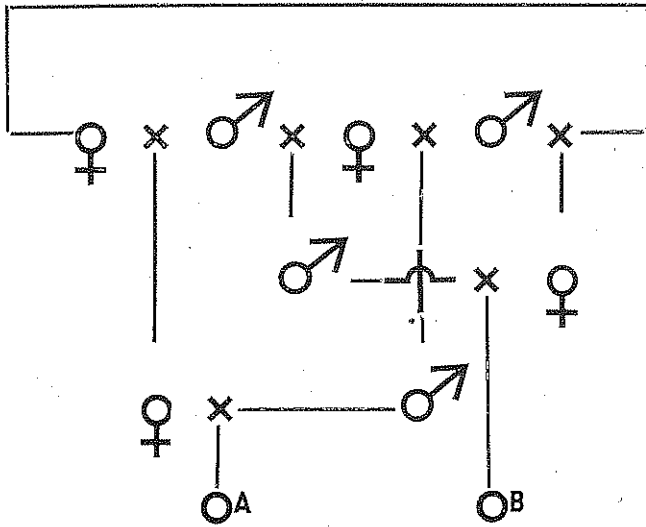


Fig. 10 The relationship symbolised by  $\begin{cases} wWw \\ wHh \\ hWh \\ hHw \end{cases}$

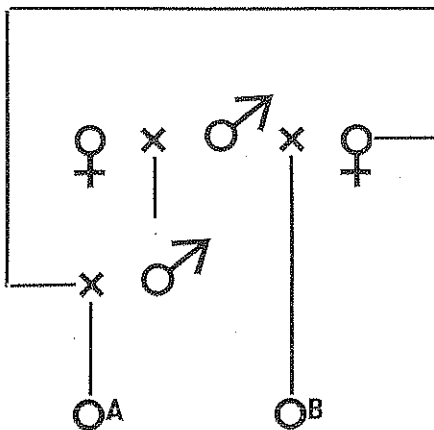


Fig. 11 The relationship symbolised by  $\begin{cases} W \\ hH \end{cases}$

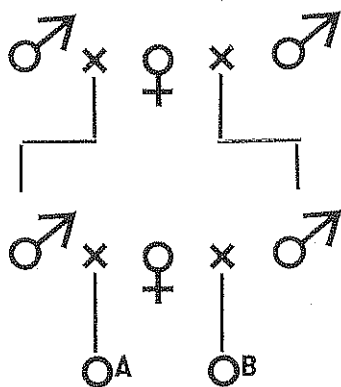


Fig. 12 The relationship symbolised by  $\left\{ \begin{matrix} W \\ hWh \end{matrix} \right.$

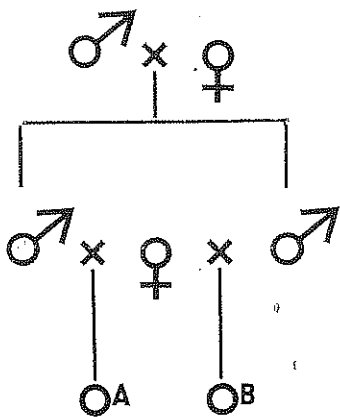


Fig. 13 The relationship symbolised by  $\left\{ \begin{matrix} W \\ hMh \end{matrix} \right.$

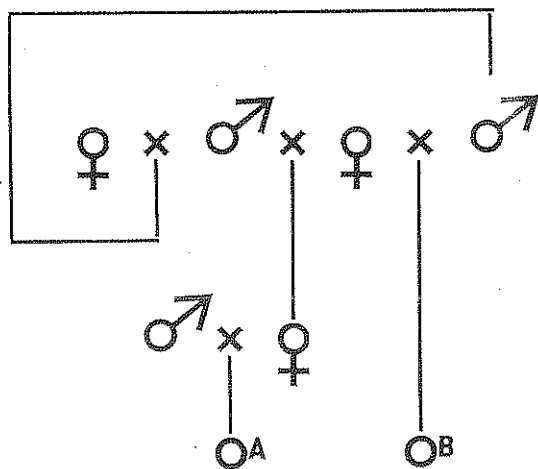


Fig. 14 The relationship symbolised by  $\left\{ \begin{matrix} wW \\ wHh \end{matrix} \right.$



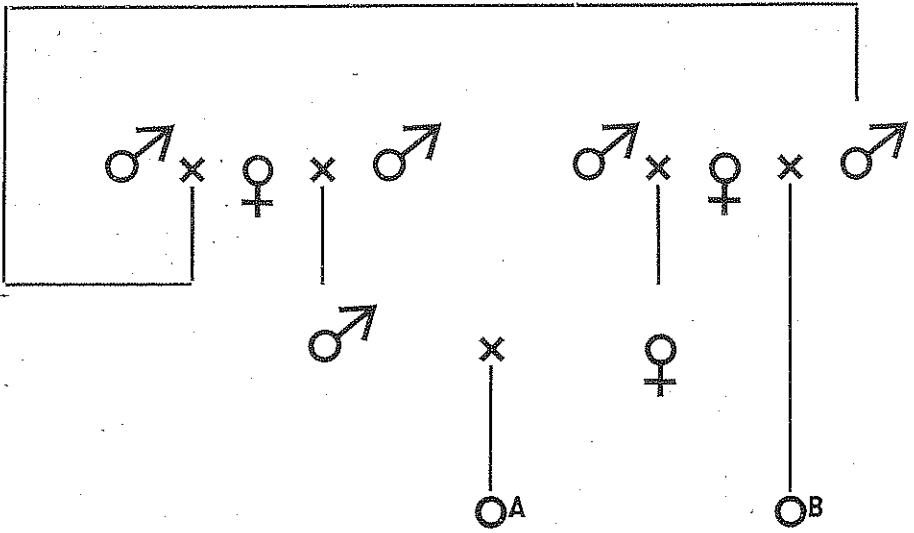


Fig. 15 The relationship symbolised by  $\begin{Bmatrix} wW \\ hWh \end{Bmatrix}$

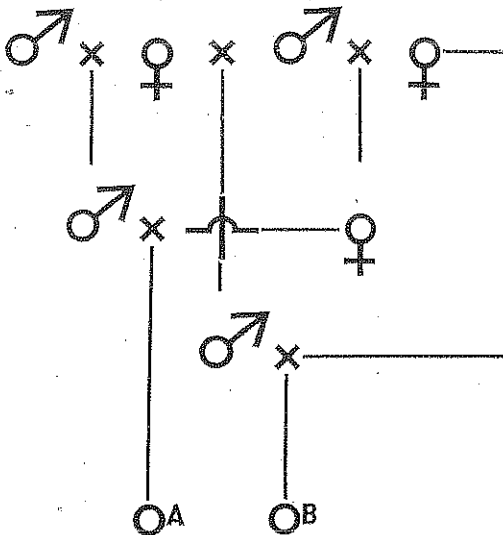


Fig. 16 The relationship symbolised by  $\begin{Bmatrix} wW \\ wHh \\ hWh \end{Bmatrix}$

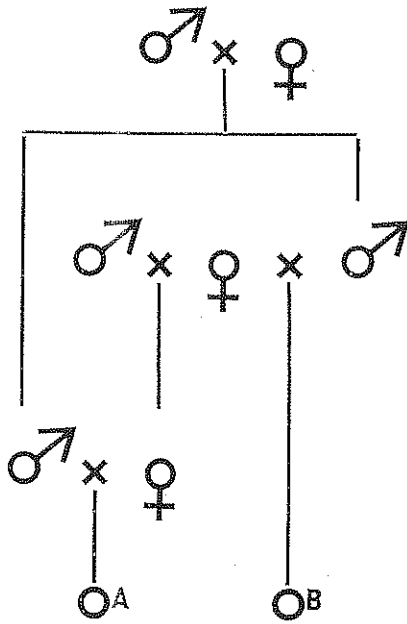


Fig. 17 The relationship symbolised by  $\begin{Bmatrix} wW \\ hMh \end{Bmatrix}$

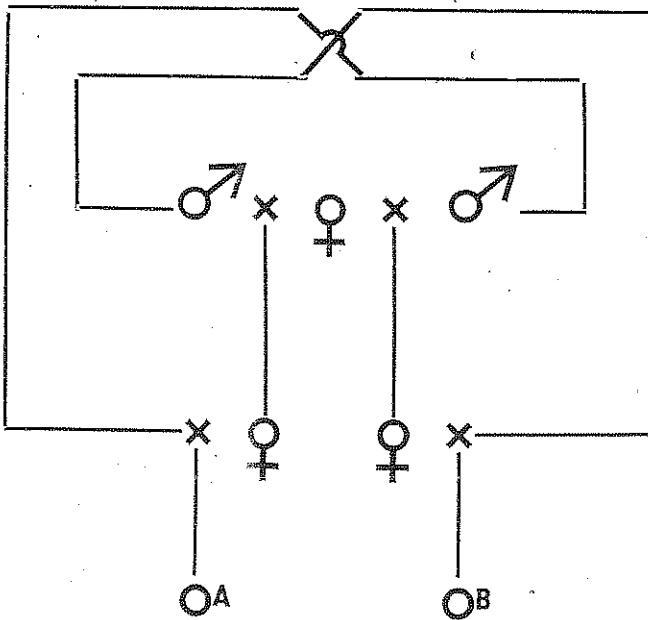


Fig. 18 The relationship symbolised by  $\begin{Bmatrix} wH \\ Hw \\ wWw \end{Bmatrix}$

and Arjuna, though legally sons of Pandu, were in fact children of their mother Kunti by different males, their relationship was  $\left. \begin{matrix} W \\ hWh \end{matrix} \right\}$ . To take a still more startling relationship, according to some Greek mythologists, after Odysseus' death his son Telemachus by Penelope married Circe, his son Telegonos by Circe married Penelope.

The children of these second marriages were in the relation  $\left. \begin{matrix} Wh \\ hWh \\ hHh \end{matrix} \right\}$ . Each, if a male, was half-uncle, half-nephew, and half-first cousin of the other. It is perhaps unlikely that this relationship, which closes our list, has occurred outside mythology.

While relationships whose symbol contains a single  $H$  or a single  $W$  are not rare, those with several such are much rarer, and those involving a triple remarriage of five persons must be very rare, even though such a chain of marriages could occur without divorce. On the other hand a cyclical remarriage (Fig. 10) must be rare, though it occurs in communities where divorce is easy and spouses-exchanged. But the sequel of two marriages between the unrelated progeny of the cyclical remarriage must be very rare indeed, whereas a marriage between two brothers and two sisters, which yields similar coefficients of relationship, is not unusual.

The relationships fall into 24 groups, in each of which the structure, as shown by the pedigree, is the same, apart from differences of sex. Hence in each group the values of  $f$  and  $F$ , which refer to autosomal genes, and are thus not affected by sex, are constant. The groups are separated in Table 1. The values of  $f$  and  $F$  may of course be the same in two groups of different structure, for example the grandparent and grandchild group and the half sib group. There is no difficulty in being sure that one has enumerated all the possible relationships in such a group. One has merely to permute the sexes of all relevant ancestors of  $A$  and  $B$  in every way consistent with the condition that the parents of any individual are of different sexes. The number of relationships in a group then ranges from 1 to 16 (subject to multiplication by 4 if the sexes of  $A$  and  $B$  are taken into account). It is a little harder to lay down rules to ensure that the enumeration of the isomorphic groups is exhaustive.

The following argument shows that there are 48 and only 48 types of first cousin relationship.  $A$  has four grandparents, his mother's mother  $C_2$ , his father's mother  $C_1$ , his mother's father  $\gamma_2$ , his father's father  $\gamma_1$ . Similarly  $B$ 's four grandparents may be labelled  $C'_2, C'_1, \gamma'_2, \gamma'_1$ .  $A$  and  $B$  may have 1, 2, 3, or 4 grandparents in common.

First consider in how many ways they may have one in common. We can choose any of  $A$ 's four grandparents, say  $C_1$ . This grandparent must be a female grandparent of  $B$ , and can be assigned to  $B$  in two ways; either as  $C'_1$  or  $C'_2$ . Thus there are 8 different relationships. We can choose two like-sexed grandparents of  $A$  in 2 ways, and assign them to  $B$  in 2 ways. So they can have two like-sexed grandparents in 4 ways. We can choose two unlike-sexed grandparents of  $A$  in 4 ways, and assign them in 4 ways. So  $A$  and  $B$  can have 2 unlike-sexed grandparents in 16 ways, and 2 grandparents in 20 ways. We can choose 3 grandparents of  $A$  in 4 ways, and assign them to  $B$  in 4 ways, making 16 possibilities. Finally if they have all 4 grandparents in common

the grandmothers may be assigned to  $B$  in 2 ways, and the grandfathers in 2 ways, making 4 in all. This agrees with the figures 8, 20, 16, and 4, given in Table 1.

However we actually used a method which can be illustrated from the relations between first cousins. We write down the 8 single path relationships:—

$wWw$ ,  $wWh$ ,  $hWw$ ,  $hWh$ ,  $wHw$ ,  $wHh$ ,  $hHw$ , and  $hHh$ .

Any one of these is compatible with any other differing from it by two or more steps. A capital letter represents two steps. Thus  $wWw$  is compatible with all the others except  $wWh$  and  $hWw$ . Thus 8 of the 28 possible pairs of paths are excluded because they involve incest, e.g.  $\left. \begin{matrix} wWw \\ wWh \end{matrix} \right\}$ . This leaves 20 admissible relationships with 2 grandparents in common. A third path may be added to each pair provided it is not incompatible with either of the first two. The triad of paths must include two with the same common capital letter. There are only 4 such pairs, and each such pair can be associated with any path with the other capital letter. For example  $\left. \begin{matrix} wWh \\ hWw \end{matrix} \right\}$  can be associated with any path including  $H$ . Thus there are 16 relationships involving 3 grandparents. Similarly each of the two compatible pairs including  $W$  can be associated with either of the two including  $H$ , giving 4 quadruple relationships. In fact we represented each single path by a point, joined the compatible points by 20 lines, and then picked out triangles and quadrilaterals with both diagonals. Two paths differing only in their capital letters are condensed, e.g.  $\left. \begin{matrix} wWw \\ wHw \end{matrix} \right\}$  to  $wMw$ . The same principles can be applied to the relationships of mixed degree, though here some multiple relationships are excluded because they involve more than 3 generations.

The calculation of coefficients of relationship is not difficult.  $B$  may be related to  $A$  by at most 4 single paths; and since a gene found in  $A$  and  $B$  can only be inherited from one of their common ancestors, the contributions of these paths to  $f$  and  $\phi$  are additive. The single paths are symbolized by  $W$ ,  $H$ , numbers 1 to 8 of degree 3, and numbers 1 to 8 of degree 4. Thus having calculated the values of  $f$  and  $\phi$  for these paths we can obtain them for all the rest by addition. Thus the values for  $\left. \begin{matrix} wMw \\ hWh \end{matrix} \right\}$  are

obtained by adding those for  $wWw$ ,  $wHw$ , and  $hWh$ . The values of  $F$  and  $\Phi$  are sums of two products of  $f$  and  $\phi$  values which may be looked up in the earlier parts of Table 1, and of the values when  $A \equiv B$ , which are given in the first line of Table 2.

The most important of the coefficients is Wright's  $f$ , which among other things, determines the biological dangers of inbreeding, and its biological advantage in reducing the risk of maternal-foetal incompatibility. As the latter, though it has probably been detected by Goldschmidt (1961), has not been calculated, we discuss it in the next section. The prohibitions against marriage with cognate relatives, if, as has been suggested, they are based on the observation that inbreeding produces more defective children than outbreeding, are not very logical, as has often been pointed out. Marriage between half brother and half sister is generally prohibited, and a union between them is criminal in many legal codes. However, by the standard of  $f$ , they are no more

closely related than niece and uncle or aunt and nephew, whose union is legal in some codes, and criminal in few or none, double first cousins (who may marry where uncle and niece may not, as in Britain) and several complex relations. In British law a man may not marry his half-niece, who is less closely related ( $f = \frac{1}{16}$ ) than his double first cousin.

THE EFFECT OF INBREEDING ON DISEASE AND DEATH DUE TO MATERNAL-FOETAL INCOMPATIBILITY

Consider an autosomal locus where a gene **A** determines the production of an antigen such that an **Aa** child may immunize an **aa** mother, and cause its own death, or more usually that of a subsequent **Aa** child. The symbol **A** is used both for genes such as **A<sub>1</sub>** which appear often to immunize a mother to her first **Aa** child, and those such as **D** which rarely immunize the mother during the first pregnancy.

If  $p$  is the frequency of **A**,  $q$  that of **a**, i.e. of all alleles not producing the antigen in question, the frequency of mothers lacking the antigen is  $q^2$ . In a random mating population a fraction  $p$  of their children, or  $pq^2$  of all children, is liable to be immunized. Of these  $p^2q^2$  are in families consisting of **Aa** children only,  $pq^3$  in families consisting of **Aa** and **aa**. In the case of genes such as **D** the former are at a considerably greater risk. If the father is a relative of the mother with given values of  $f$  and  $F$ , the frequency of **Aa** among the children of **aa** mothers is reduced from  $p$  to  $(1-2f)p$ . The fraction belonging to all-**Aa** families is reduced from  $p^2$  to  $(1-4f+F)p^2$ , while that belonging to mixed families is changed from  $pq$  to  $p[q+2f(p-q)-Fp]$ , which may be an increase or decrease according to the value of  $p$ . If  $K$  of the **Aa** children of homozygous, and  $k$  of the children of heterozygous fathers are killed by incompatibility, the death-rate from this cause is  $pq^2(Kp+kq)$  when parents are unrelated, and

$$pq^2[Kp+kq-f(2Kp-kp+kq)+F(K-k)p]$$

when they are related. Thus inbreeding saves the lives of a fraction

$$f + \frac{(f-F)(K-k)p}{Kp+kq}$$

of the babies which would otherwise die from the effect of incompatibility.  $f > F$  and  $K > k$ , so the fraction exceeds  $f$ , but cannot exceed  $2f-F$ . This however is the fraction saved at any one locus. If the number of independent loci concerned is large enough, it is conceivable that the death-rate may be reduced quite considerably by cousin marriage.

Sex-linked genes responsible for human antigens are not yet known.\* Still less is there any evidence that such genes are ever responsible for incompatibility between mother and foetus. However it is interesting to calculate what effect they have if they exist. Let **S** and **s** be a pair of sex-linked allelomorphs, or groups of allelomorphs, such that **S** determines the production of an antigen capable of immunizing **ss** mothers, while **s** does not. A **ss** mother cannot bear **S** sons, but may bear **Ss** daughters, who may be eliminated. Let  $p$  and  $q$  be the frequencies of **S** and **s**, and  $k$  the fraction of **Ss** daughters of **ss** mothers eliminated. The fraction of daughters eliminated if parents

\* We learn that one has at last been discovered.

are unrelated is clearly  $kpq^2$ , and it can be seen that there is unstable equilibrium when  $p=q=\frac{1}{2}$ , as in the autosomal case. The frequency of males among the surviving offspring would thus be  $\frac{1}{2-kpq^2}$  if no other causes were disturbing the sex ratio.

If the parents are related, the frequency of *Ss* among the daughters of *ss* mothers is reduced from  $p$  to  $(1-\phi)p$  where  $\phi$  is the coefficient of relationship of the parents. Thus the frequency of males would be reduced from  $(2-kpq^2)^{-1}$  to  $[2-k(1-\phi)pq^2]^{-1}$ . Goldschmidt however found more males when the parents were related. So incompatibility, if it accounts for a lower abortion rate, cannot account for a higher frequency of males when parents are related. If  $p=\frac{1}{2}$ , which gives the maximal elimination, and  $k=0.1$ , which is very high, the frequency of males would only be 50.373%, and if the coefficient of sex-linked relationship of parents were  $1/8$ , it would only be reduced to 50.326%, which could hardly be verified on a sample less than a million. There might be several such loci on the *X* chromosome, but a high mortality rate and a high frequency of the rarer allele could seldom coexist. Even if, between them, they accounted for the whole excess of males observed, inbreeding would rarely reduce the ratio by even one eighth of the way towards equality. We conclude that such effects, if they occur, are unimportant.

The effect of inbreeding in raising the male frequency, if it is confirmed, is perhaps more likely to be due to the same group of causes which eliminate male mammals, and in general members of the heterogametic sex, in interspecific hybrids (Haldane, 1922).

#### THE EFFECT OF MONOZYGOTIC TWINNING

If *B* is *A*'s monozygotic twin, the effect on the coefficients of relationship is as shown in the first line of Table 2. If a pair of like-sexed sibs are monozygotic twins they are believed to be genetically identical. If any pair of "paths" connecting *B* to *A* passes through a pair of whole brothers or sisters, these may be monozygotic twins. In double first cousinship of the first type, either the sisters, the brothers, or both, may be monozygotic twins. The relationships which can be transformed by monozygotic twinning are listed in Table 2. The first one can of course only be transformed if *A* and *B* are of like sex, the second if *B* is a woman, the third if *A* is a woman, the fourth if *B* is a man and the fifth if *A* is a man. Altogether 18 relationships can be so transformed. The second column gives the original value of *f*, the fourth and later those of the transformed relationship. The value of *f* is always increased, but never more than doubled. That of *F* can be increased up to four times. The marriage of two pairs of monozygotic twins may not be as rare as might be thought. A biometric study of the resemblance between the children of monozygotic twins would be well worth carrying out.

#### RELATIONSHIPS WHEN RELATIVES ARE INBRED

We shall not consider these in any detail, but it may be instructive to work out the number of first cousinships possible if *A*, *B*, or both are inbred. *A* may have only 3

Table 2. *Enhancement of relationship by monozygotic twinning*

Original relationship	$f$	Enhanced relationship	$f$	$F$	$\phi_{11}$	$\phi_{12}$	$\phi_{21}$	$\phi_{22}$	$\Phi$
$M$	$\frac{1}{4}$	Identity	$\frac{1}{2}$	1	1	..	..	$\frac{1}{2}$	1
$wM$	$\frac{1}{8}$	Mother	$\frac{1}{4}$	0	..	$\frac{1}{2}$	..	$\frac{1}{4}$	0
$Mw$	..	Woman's child	..	..	0	..	$\frac{1}{2}$	..	0
$hM$	..	Father	..	..	0	$\frac{1}{2}$	..	..	..
$Mh$	..	Man's child	..	..	0	..	..	..	..
$wMw$	$\frac{1}{16}$	$W$	$\frac{1}{8}$	0	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	0
$hMh$	..	$H$	..	..	0	0	0	$\frac{1}{4}$	0
$wMw$ } $hWh$ }	$\frac{1}{8}$	$W$ } $hWh$ }	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
$wMw$ } $hHh$ }	..	$W$ } $hHh$ }	..	..	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	0
$hMh$ } $wWw$ }	..	$H$ } $wWw$ }	..	..	$\frac{1}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{3}{8}$	$\frac{1}{8}$
$hMh$ } $wHw$ }	..	$H$ } $wHw$ }	..	..	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{5}{16}$	$\frac{1}{4}$
$wMw$ } $hMh$ }	$\frac{1}{8}$	$W$ } $hMh$ }	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{4}$
..	..	$H$ } $wMw$ }	..	..	$\frac{3}{8}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{3}{8}$	$\frac{3}{8}$
..	..	$M$ } $M$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{3}{8}$	$\frac{1}{2}$
$W$ } $hMh$ }	$\frac{1}{16}$	$M$	..	..	..	..	..	..	..
$H$ } $wMw$ }	..	$M$	..	..	..	..	..	..	..
$wW$ } $hMh$ }	$\frac{1}{8}$	$H$ } $wW$ }	$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{5}{16}$	$\frac{1}{4}$
$Ww$ } $hMh$ }	..	$H$ } $Ww$ }	..	..	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{5}{16}$	$\frac{1}{4}$
$hH$ } $wMw$ }	..	$W$ } $hH$ }	..	..	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	0
$Hh$ } $wMw$ }	..	$W$ } $Hh$ }	..	..	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{8}$	0

grandparents in two ways. His double grandfather had a son and daughter by different women, and  $A$  is the offspring of their union. Or he may have only one grandmother as a result of a union between her offspring by two men. In either case the three grandparents can be specified uniquely.  $A$  can have only two grandparents in three ways. His grandfather may have united with a daughter, and is therefore  $A$ 's father and grandfather. Or his grandmother may have united with a son. We do not consider these possibilities further, as they give rise to mixed relationships of degree 3 and 4. Finally  $A$  may be the offspring of the union of a whole brother and sister.

This possibility will be considered. All these possibilities are of course realised in animal breeding.

Table 3. Summary of Tables 1 and 2

Degree of relationship	Symmetrical relationships	Pairs of converse relationships	Number enhanced by monozygosity
1	0	1	0
2	3	2	1
3	2	9	4
4	24	12	7
2+3	0	2	0
2+4	6	0	2
3+4	2	20	4
	37	46	18

It is convenient to denote the relationships where  $A$  has  $m$  grandparents and  $B$  has  $n$  by  $(m, n)$ . We have shown that there are 48 relationships of class  $(4, 4)$ . Let us now find the number in class  $(3, 4)$ . First consider the relationships with 1 grandparent in common. If  $A$  has only one grandfather he can be assigned to  $B$  in 2 ways. But  $A$ 's grandmother can be chosen in 2 ways and assigned in 2. So they may have one grandparent in common in 6 ways, with 6 more when  $A$  has only one grandmother, making 12. Again if  $A$  has only one grandfather we can choose two grandmothers in one way and assign them to  $B$  in 2 ways; we can choose a grandfather and grandmother in 2 ways and assign them in 4. Similarly if  $A$  has only one grandmother. Thus  $A$  and  $B$  can have 2 common grandparents in 20 ways. Similarly  $A$ 's 3 grandparents may be assigned in 4 ways if he has one grandmother, or 8 in all. The total number of cousinships of class  $(3, 4)$  is thus  $12 + 20 + 8$ , or 40.

Similar calculations may be made for other classes, and we find the following numbers

$(4, 4)$	48
$(3, 4)$ and $(4, 3)$	80
$(2, 4)$ and $(4, 2)$	16
$(3, 3)$	40
$(2, 3)$ and $(3, 2)$	20
$(2, 2)$	3
	207

Thus the number of possible first cousin-ships has been increased from 48 to 207, or 828 if the sexes of  $A$  and  $B$  are considered. The grand total of all relationships would be considerably increased, since new relationships of mixed degree are possible,



for example  $A$  may be  $B$ 's parent and grandparent, parent and half-sib, and so on. Our  $h, w$  symbolism is not adapted to describe relationships involving inbreeding of either relative, that is to say relation through a line of intermediaries which forks.

#### RELATIONSHIPS OF HIGHER DEGREE

It is quite possible to enumerate relationships of higher degree, and to calculate their coefficients. We have not attempted this task for two reasons. The first is its gigantic character. As will be seen, a list of relationships between second cousins on the lines of Table 1 would occupy several volumes. The second is that as soon as we reach asymmetrical relations of degree 4 such as that of great-uncle, or relations of higher degree such as first cousin once removed, it becomes possible for  $A$  or  $B$  to be inbred, and related through chains of relatives which split. We shall merely calculate the number of distinct relationships between second cousins which do not involve inbreeding, so that both  $A$  and  $B$  have 8 distinct grandparents. Clearly they are all built up of 32 constituents such as  $whWhh$ , though at most 8 of these can be combined, since there are at most 8 common grandparents. Let the great-grandmothers of  $A$  be  $C_1, C_2, C_3, C_4$ , the great-grandfathers  $\gamma_1, \gamma_2, \gamma_3, \gamma_4$ , each defined by her or his relation to  $A$ . Thus  $C_2$  might be  $A$ 's mother's father's mother. Let  $C'_1, C'_2, C'_3, C'_4, \gamma'_1, \gamma'_2, \gamma'_3, \gamma'_4$  be the great grandparents of  $B$ , similarly defined. From 1 to 8 of these may be common great grandparents of both. Consider the grandmothers. If a single one is common to  $A$  and  $B$  this can occur in  $4^2$  or 16 ways, for that of  $A$  can be any of  $C_1, C_2, C_3$ , and  $C_4$ , and that of  $B$  can be any one of  $C'_1, C'_2, C'_3$  and  $C'_4$ . Thus the same woman could be  $A$ 's mother's father's mother and  $B$ 's father's father's mother. Similarly a second identical pair can be chosen in  $3^2=9$  ways, but since the order of the pairs is irrelevant we have  $16 \times 9 \div 2$  or 72 possibilities. Similarly 3 identities can be chosen in  $4^2 \cdot 3^2 \cdot 2^2 \div 3!$ , or 96 ways, and four identities in  $4^2 \cdot 3^2 \cdot 2^2 \cdot 1^2 \div 4!$ , or 24 ways.

In fact the identity of  $i$  great grandmothers allows of  $\frac{(4!)^2}{[(4-i)!]^2 i!}$  possibilities. The same is clearly true for the great grandfathers. Now suppose  $A$  and  $B$  have 5 great-grandparents in common, 4 may be great grandmothers and 1 great-grandfather, or 1 great-grandmother and 4 great-grandfathers, each giving  $24 \times 16$ , or 384 possibilities. Or they may have 3 great-grandmothers and 2 great-grandfathers, or 2 and 3, in common, each giving  $72 \times 96$ , or 6912 possibilities. We thus have the possibilities given in Table 4.

There are thus 43,680 or  $2^5 \cdot 3 \cdot 5 \cdot 7 \cdot 13$  distinct relationships when neither  $A$  nor  $B$  is inbred. But  $A$ 's or  $B$ 's parents may, without incest, be any one of the 48 types of first cousin, descended from only 7 to 4 great-grandparents. When allowance is made for this there may be about 9 million types of second cousin.

#### DISCUSSION

Our main results are summarized in Table 3. Perhaps the most unexpected is the large number of possible relationships of mixed degrees 3 and 4. Some of these may

Table 4. Possible relations of outbred second cousins

Number of common greatgrandparents	Partitions	Possible relationships	Total
1	0+1	$2 \times 16$	32
2	0+2, 1+1	$2 \times 72 + 16^2$	400
3	0+3, 1+2	$2 \times 96 + 2 \times 16 \times 72$	2,496
4	0+4, 1+3, 2+2	$2 \times 24 + 2 \times 16 \times 96 + 72^2$	8,304
5	1+4, 2+3	$2 \times 16 \times 24 + 2 \times 72 \times 96$	14,592
6	2+4, 3+3	$2 \times 72 \times 24 + 96^2$	12,672
7	3+4	$2 \times 96 \times 24$	4,608
8	4+4	$24^2$	576
			43,680

not be very rare. Where it is permitted, there is nothing surprising in a widower marrying a woman, and his son by another marriage marrying her younger sister. The children of these marriages are in the relationship symbolized by  $\left. \begin{matrix} Hh \\ wMw \end{matrix} \right\}$ .

We are aware that we may have made errors both by omitting relationships permitted by our hypothesis, by miscalculation, or by the overlooking of misprints. We shall be thankful to receive corrections, and to publish them if they are accepted. Our symbolism may be found unacceptable. We have given reasons for preferring it to a bulkier if more logical symbolism, and for using  $w$  and  $h$  rather than  $f$  and  $m$ ,  $m$  and  $f$ , or  $m$  and  $p$ . It has the grave demerits of not covering ancestral relationships or their converses, relations beyond the fourth degree, or relationships involving incest. It has however the merit that it can readily be extended to cover the distinction between older and younger brothers or sisters where this is sociologically important. If by putting a sign above or below that of the common ancestor or ancestors we denote younger and elder sibs, while an asterisk denotes twins, this need can be met. Thus  $\overline{W}$  would denote a younger maternal half sib,  $\underline{Mw}$  the child of an elder full sister,  $wM^*$  a twin of  $A$ 's mother, and so on.

There is a very serious gap between genetics and anthropology, and anything which can help to bridge that gap is worth attempting.

#### SUMMARY

The logical structure of human relationships is discussed. When the relatives are not inbred their genetical implications can be summarized by four coefficients of relationship, namely Wright's coefficient of single autosomal relationship, a coefficient of double autosomal relationship, a coefficient of single sex-linked relationship, and one of double sex-linked relationship between women only. A simple symbolism

for human relationships is developed. There are 516 possible relationships between  $A$  and  $B$ , not involving an ancestor of either more remote than a grandparent, and not involving incest. Table 1 gives the coefficients of relationship for all of them. 192 are relationships between first cousins. In 66 cases the coefficients may be raised by monozygotic twinning. The effect of relationship on incompatibility between mother and foetus is described. There is a brief discussion of relationships involving incest, and those between second cousins.

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