

SELF-INCOMPATIBILITY SYSTEMS IN ANGIOSPERMS

I. THEORY

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I. INTRODUCTION

A SURVEY by Lewis (1944) classified all known incompatible species into two systems:

(i) with multiple allelomorphs; one locus in diploids; sporophytic control of style reaction (with independent action of different alleles) and gametophytic control of the pollen; always homostyled.

(ii) with two alleles per locus; one or two loci; sporophytic control of both pollen and style (alleles showing dominance); with one exception (*Capsella*) heterostyled.

Lewis argued that other combinations of these characteristics would for one reason or another be handicapped and that further research would be unlikely to unearth any new incompatibility system.

On the other hand, Mather (1944) considered that novel systems might yet be found and argued as follows:

“Such a system would presumably use both the multiple allelomorphs of the haplo-diploid and the co-ordination of gene action necessary to impress a somatically determined behaviour on the male gametes in the way shown by the diplo-diploid. It is, however, not yet clear how, or even whether, such a system is a developmental possibility.”

Experiments conducted by the author into the genetics of self-incompatibility in the Crucifers *Raphanus sativus* and *Brassica campestris* suggested that these species did not readily fit into an oppositional system such as found in *Nicotiana* by East and Mangelsdorf (1925). Neither were they heterostyled. The literature on other Crucifers previously studied showed anomalous conditions also in *Brassica oleracea*

(Kakizaki, 1930 and Sears, 1937), *Cardamine pratensis* (Correns, 1913; Beatus, 1931) and *Capsella grandiflora* (Riley, 1936).

It seemed desirable therefore, to derive from first principles all conceivable incompatibility systems and to test their ability to function adequately. While engaged on this work papers appeared on incompatibility in two species of Compositae, *Parthenium argentatum* (Gerstel, 1950) and *Crepis foetida* (Hughes and Babcock, 1950). Here not only had the inadequacy of the *Nicotiana* system become apparent but a hitherto undescribed system had been invoked which appeared adequate to account for the data. The need for a return to first principles seemed more urgent than ever.

The highly dispersed incidence of self-incompatibility throughout the Angiosperms is an indication that it has arisen *de novo* a large number of times. (This has been contested by Whitehouse (1950) whose arguments will be considered later.) In which case it would be only to be expected that all incompatibility systems (just as all floral mechanisms promoting cross-pollination) which could withstand the rigours of natural selection and which were physiologically possible might be encountered somewhere among the families of flowering plants.

2. MINIMUM REQUIREMENTS OF AN INCOMPATIBILITY SYSTEM

The primary function of self-incompatibility is the avoidance of self-fertilisation. It differs from all other mechanisms such as protandry, protogyny, monoecy, dioecy and all special floral mechanisms which achieve the same end more or less effectively, in that while all the rest do so by interposing some *mechanical barrier to self-pollination* self-incompatibility acts at a later stage, by interposing a *physiological barrier between self-pollination and self-fertilisation*.

In *Oenothera organensis* (Emerson, 1938) the difference in growth of compatible and incompatible pollen tubes is very marked. Compatible tubes rapidly grow down the very long style, while incompatible tubes do not grow long enough to empty the pollen grain. Such a rigorous inhibition of self-pollen is not necessary, however, for self-fertilisation to be suppressed under natural conditions. Except when the pollinator (wind or insects) is excluded there will be enough compatible pollen on the stigma to grow down the style before self-pollen unless the growth rate of self-pollen tubes approaches closely to that of fully compatible pollen or unless self-pollination occurs in the bud. Even when self-pollen tubes grow fast enough for self-fertilisation under natural conditions to be a common occurrence the degree of cross-fertilisation may still be enough for the requirements of the species. No one doubts the selective value of protandry and monoecy which only partially reduce self-fertilisation. The natural frequency of partially self-fertile incompatible species is high. This can be seen from the literature in the number of experimenters on self-incompatibility whose work has been hampered by pseudo-compatibility. Even an incompatibility system which acted in such a way that a proportion of

the individuals were fully self-fertile might be favoured by natural selection. As an outbreeding mechanism it would be comparable in efficiency to the widespread gynodioecy developed in the Labiatae and Caryophyllaceae.

Whatever the details of any genetically determined incompatibility system, there must always be cross-incompatibility between genetically similar individuals. Such cross-incompatibility is only an outbreeding mechanism when it reduces the chances of sib mating relative to mating with non-sibs. In dimorphic heterostyled species the cross-incompatibility can have no selective value because the proportion of the two mating types among sibs (1:1) is the same as in the whole population. Such cross-incompatibility must be merely a fortuitous by-product of the breeding mechanism.

In a species like *Nicotiana sanderae* with a large number of oppositional alleles, cross-incompatibility between unrelated individuals will be negligible. The progeny of two individuals with no common allele falls into four cross-compatible classes though only half the *pollen* of sibs (owing to half-compatibility between plants with one common allele) will be compatible. Relative to the general population the chances of sib mating would, therefore, be reduced by a half. This will have a much smaller effect on the degree of outbreeding of the species than the complete inhibition of self-fertilisation. It is unlikely, therefore, that the effect of any particular incompatibility system on cross-incompatibility will play an important role in determining its overall selective value. Mather (1944) also holds that in flowering plants its effect on sib mating is likely to be a trivial consideration in determining the selective value of a mating system.

3. COMPLEMENTARY AND OPPOSITIONAL SYSTEMS

There would seem to be two basic ways of determining self-incompatibility, the stimulation of unlike genotypes and the inhibition of like genotypes. These may be distinguished by the terms complementary and oppositional, the latter being East's original term.

A complementary system involves the mutual dependence of a pair of genotypes for the completion of sexual reproduction. In this way, male and female individuals in dioecious species are complementary though here not only the physiology, but the morphology also are complementary. Something closer to the incompatibility of higher plants is encountered in heterothallic Mucorales in which the presence of the complementary mating type stimulates the development of sex organs. Moewus' account (1939) of heterothally in *Chlamydomonas* also indicates a complementary relationship between mating types. Some of the heterostyled flowering plants appear to have a complementary system, as for example, *Linum grandiflorum* (Lewis, 1943a) and *Forsythia intermedia* (Moewus, 1950).

A mechanical model of the complementary relationship could be given by lock and key, the key of the pollen of one mating group fitting

the lock of the other. Such a model emphasises the limitations to the number of possible complementary mating types. Even with three types, each type must carry with it the "keys" to the "locks" of the two others. It is difficult at first sight to see how even a three-type complementary system could work, but the morphological arrangement in tristylous *Lythrum salicaria* provides the clue. Each form has one style length (one lock) and two anther heights (two keys). As each anther height from whichever form is only compatible on one style the parallel with the "key and lock" theory is complete. Each anther height corresponds to a single "key" so that each form carries two "keys" by virtue of its two anther levels. Apparently both "keys" cannot be borne in the same anther and one "key" cannot fit two "locks". The principle is illustrated in fig. 1.

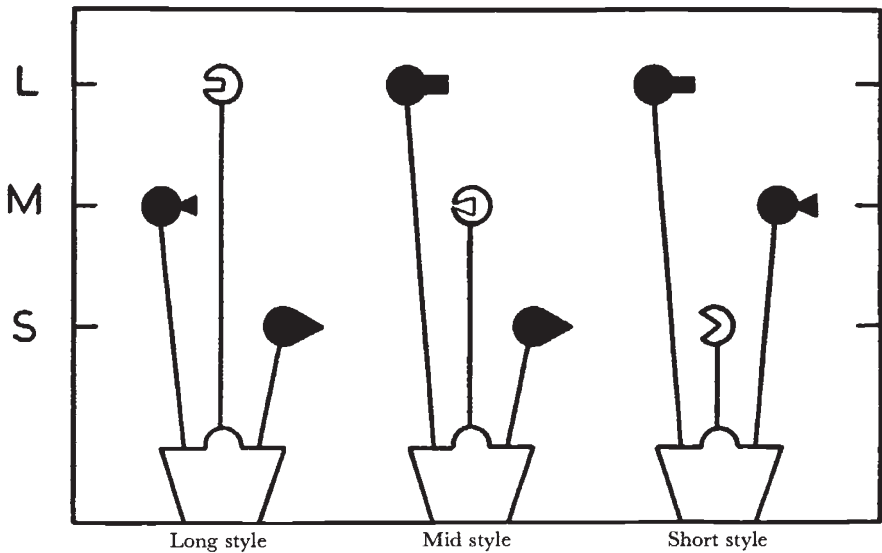


FIG. 1.—Symbolic representation of a complementary incompatibility mechanism in a trimorphic heterostyled species. White circle=stigma; black circle=anther.

Oppositional systems depend upon an antagonism between style and pollen of like genotypes. East (1929) was the first to postulate the antigen-anti-body reaction to explain this, the pollen producing the antigen and the style the anti-body. No direct evidence for the correctness of this hypothesis has so far been published, but in the absence of a better hypothesis we are justified in using it as the underlying assumption in our discussion of oppositional systems.¹

The most important distinction between the reactive compounds responsible for incompatibility and the antigen-anti-body system of serology is that the antigen does not induce the production of the anti-body; *both* are preformed. In this they are more like the A B O blood groups in man in which O blood contains anti- A and anti- B before the addition of the A and B antigens. Also one cannot objectively

decide in the case of incompatibility which would be the antigen and which the anti-body. Since, however, it is the pollen whose growth is inhibited, we may take it as a working hypothesis that the pollen produces the antigen which is coagulated by the stylar anti-body.

That there is a positive antagonism between style and self-pollen has been shown by Lewis (1942) in *Prunus*, *Oenothera* and *Primula*. The growth of compatible pollen was greater at high than at low temperature, but incompatible pollen grew faster at the low temperatures.

The present classification of incompatibility systems cuts across previous ones such as hetero- versus homomorphic (*e.g.* Lewis, 1944) or haplo-diploid versus diplo-diploid (Mather, 1944). The author regards this distinction between complementary and oppositional systems as the fundamental one. The relations between different methods of classi-

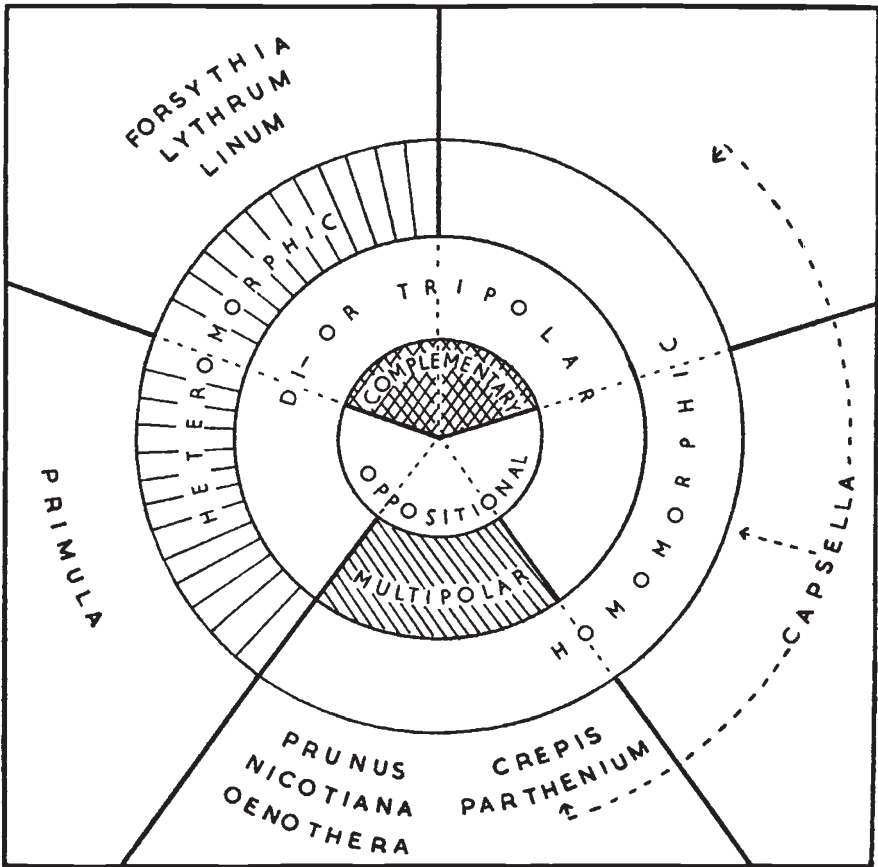


FIG. 2.—A comparison of three classifications of incompatibility systems.

fication are shown in fig. 2 with a few examples. Mather's haplo-diploid versus diplo-diploid classification is omitted here as apart from heteromorphous systems where the determination is probably always diplo-diploid, either of his classes could work in conjunction with any other combination of classes.

If the combinations of the three pairs of classes were random, there would be 8 different combinations. However, heteromorphism and complementary relations of the mating groups both exclude multipolar systems so that only five combinations are theoretically possible. Examples of three amongst flowering plants are well established: complementary, di- or tripolar, heteromorphic; oppositional, dipolar, heteromorphic; and oppositional, multipolar, homomorphic. The combination of tripolar and homomorphic is only known in the apparently anomalous species *Capsella grandiflora*. Here the close genetical similarity to *Lythrum* indicates the possibility of a complementary system, but the situation in *Capsella* will be discussed at length in a second paper. There are no other examples of Angiosperms in either of the remaining combinations though *Mucor* is an example among cryptogams of a complementary dipolar homomorphic system.

4. ORIGIN OF INCOMPATIBILITY

Complementary systems could be determined in so many different ways (the few cases so far known, e.g. *Linum*, *Lythrum* and *Forsythia*, illustrate this) that a general discussion of their evolution would seem to be of little value. In any case they seem to represent only a small section of all incompatible species. In the remainder of this paper, therefore, we shall concern ourselves only with oppositional systems.

Whitehouse (1950) has argued that multiple-allelomorph incompatibility probably arose only once in the evolution of the Angiosperms, at the point of origin when the style first developed. His argument is based upon the beliefs that (a) the selective powers the style is able to exert upon pollen tubes are its main function and (b) that since at least three **S**-alleles are necessary for a *Nicotiana* incompatibility system to become workable, such incompatibility could only arise by the simultaneous mutation of the prototype **S**-gene to three new active alleles. This is held to be very improbable. I do not feel, however, that this argument is very sound. In the first place to obtain a fully working self-incompatible species from a previously self-fertile one not only are three **S**-alleles necessary, but there must be the division of labour between style, producing anti-body and pollen, producing antigen. In a word there must be the evolution of a large number of modifiers as well. It is unlikely that self-incompatibility when it first arose would be fully effective any more than any other newly evolving function, but much more probable that it emerged gradually without any coincidence of rare mutations being necessary. In the second place if we accept his argument that the origin of incompatibility is a very improbable event, how much less likely is it to arise among the few incipient Angiosperm individuals at the point of origin of the phylum than among the enormous number of Angiosperms living to-day?

Whitehouse further bases his argument on the assumption that the absence of a style in Gymnosperms precludes self-incompatibility based on a styler reaction. Reference to Coulter and Chamberlain (1910)

shows that it is typical of gymnosperms for pollen tubes to be compelled to grow through a well-developed nucellus before fertilisation is possible. Since in *Capsella* (Riley, 1936) and *Parthenium* (Gerstel and Riner, 1950) a single layer of cells in the stigma is sufficient to inhibit self-pollen, the massive nucellus of most gymnosperms should be quite capable of acting as a physiological sieve for pollen tubes. The absence of a style in gymnosperms is not, therefore, a sufficient explanation of the absence of self-incompatibility from this phylum (if it is indeed absent).²

We shall now propose an alternative theory of the evolution of incompatibility. Let us consider a species in which there is a rather loosely operating outbreeding mechanism, such as a morphological adaptation of the flowers conducive to cross-pollination and let us assume that the environment is one in which more rigorous outbreeding has a selective advantage.

In any outbreeding population, many phenotypes differing serologically may co-exist. This is known for example in man (Race and Sanger, 1950) and cattle (Owen *et al.*, 1945) and it might be expected that similar situations would hold in plants though they have not yet been found.

In man it is known that several loci are involved in this variation. The large number of serological types in cattle points to a similar conclusion. It is not illogical to suppose that genetically heterogeneous plant populations would also vary serologically in a similar way. With such raw material already available all that would be needed to produce a primitive oppositional incompatibility system is a division of labour so that the style produced anti-bodies to those antigens in the pollen for which the population was heterogeneous. The production of anti-bodies to antigens for which the population was homogeneous would merely make the plant female-sterile. This anti-body production would, therefore, have to have a measure of specificity from the start, but if, at the time of origin of the incompatibility the population was heterogeneous for several antigens there could be several "S-loci", each locus producing alternative pairs of antigens (and anti-bodies). Allowing for the qualitative differences between all incompatibility alleles and loci, this is a close approach to a typical polygenic system.

5. DEVELOPMENT OF INCOMPATIBILITY

At the time of origin the incompatibility would probably not be at full strength though even then it might be adequate for the requirements of the species. In which case one might expect to find species which had stabilised at this evolutionary level. Characteristic of such species would be a high degree of pseudo-compatibility with nevertheless consistently better setting on crossing than on selfing. If several antigen loci were involved, compatibility between sibs would vary according to the number of common alleles, but would be intermediate between selfing and crossing with unrelated plants. Further analysis

of such species would be difficult because of the pseudo-compatibility.

If, however, such a weak system were inadequate for the requirements of the species it could be improved upon in two ways, by the selection of non-specific modifiers increasing the effectiveness of all loci, or of specific modifiers increasing the effectiveness of one or two loci at the expense of the rest.

The first could proceed as far as complete incompatibility dependent on the additive effects of all the loci or complete incompatibility produced by correspondence at any one locus. Where all loci had to act simultaneously cross-compatibility might vary in a graded series according to the number of common antigens. If, however, there were (as might well be) a critical threshold strength of the reaction below which all pollinations appeared fully compatible, identity in more than a critical number of antigens would give incompatibility, less than that, compatibility. The results in such a species would probably be difficult to interpret by any clear-cut scheme especially if different loci varied in the strength of their reactions.

The simplest case would be when all the loci acted independently, additively and with equal strength, identity at all loci being necessary for full incompatibility. Cross-compatibility between sibs from a cross between parents with two active loci only and no alleles in common would be as follows. There would be 16 genotypes and out of every 16 cross-pollinations:

With gametophytic control of pollen there would be:

- 9 fully compatible, at least one quarter of the pollen having no allele in common with the style.
- 6 partially compatible, at least one quarter of the pollen having only one allele in common with the style.
- 1 incompatible.

With sporophytic control of the pollen and independent action of the alleles there would be:

- 1 pollination fully cross-compatible (no common allele).
- 4 highly cross-compatible (1 common allele).
- 6 half compatible (2 common alleles).
- 4 weakly incompatible (3 common alleles).
- 1 fully incompatible (4 common alleles).

With more than two loci an even more finely graded series of compatibilities would be possible.

Selection of non-specific modifiers could reach the point where identity at a single locus was sufficient for full incompatibility. Cross-compatibility between sibs would be increasingly rare as selection proceeded or with increasing numbers of active loci. With gametophytic control of pollen and n loci the proportion of cross-incompatibility between sibs whose parents had no allele in common would be

$$\frac{1 + \frac{3}{4} + \left(\frac{3}{4}\right)^2 + \dots + \left(\frac{3}{4}\right)^{n-1}}{4}$$

With 8 loci it would be 0.000. With sporophytic control and independence it would rise much more rapidly.

This situation resembles that in polyploids except that since in that case the loci are duplicated it is possible for the same allele to occur at either locus so that the incompatibility reaction could be exerted between different loci. This would, however, be expected to be rare except in recent autotetraploids or in species where the number of possible alleles was low. The evidence so far is that except in heteromorphic species the number of alleles is very high indeed.

The second way of improving the efficiency of a polygenic system with initially incomplete efficiency of each locus would be the selection of specific modifiers acting upon one or perhaps two loci. This is the type of incompatibility hitherto assumed to be generally applicable. An outwardly similar result would be obtained if the several active loci, as a result of translocations and inversions, came to be within a single tight linkage group. Unless, however, complete identity of all the units in such a "locus" was necessary for full incompatibility there would be cross-incompatibility between non-identical compound "alleles".

6. VARIATIONS ON THE OLIGOGENIC THEME

Oligogenic incompatibility is not only the one generally recognised: it is probably in fact the most widespread, the multigenic systems discussed above being intermediate stages in the evolution of fully developed oligogenic systems. It is also the simplest type theoretically and, therefore, the most suitable medium for a discussion of further modifications in the detailed working of the incompatibility reaction.

The possible alternatives, sporophytic and gametophytic (or diploid and haploid) control have already been mentioned. Although the pollen is haploid not all the behaviour of the pollen need necessarily be determined by its own haploid nucleus. Much of the cytoplasm and possibly the entire wall of the pollen grain will have been determined sporophytically, by the constitution of the pollen mother cells or even the tapetal cells. The reaction of the style must be diploid. It is just conceivable, however, that in the absence of a style reaction the embryo sacs themselves might be able to exert an inhibitory influence on pollen tubes of like constitution.

When there is gametophytic control in a diploid species there is no possibility of interaction between pairs of **S**-alleles because they will always occur singly. But as Lewis has shown (1947), in tetraploid species with diploid pollen there is such a possibility and, moreover, it exists. Just the same possibilities arise in diploid species wherever there is sporophytic control in style or pollen. Lewis found in tetraploid *Oenothera* that the interaction could manifest itself in two ways which he called competition and dominance. With competition both alleles were weakened; with dominance only one was inactive. Since the dominance could equally well be regarded as the result of competition

in which the weaker allele was suppressed, I prefer to use the more explicit terms mutual weakening and dominance.

In *Oenothera* the mutual weakening in heterozygous pollen grains, while increasing the tube length in self-pollinated styles did not lead to self-fertility. In other species such as *Trifolium repens* (Atwood, 1944) and *Pyrus communis* (Crane and Thomas, 1939) self-fertility is produced. In diploid species with sporophytic control of the pollen, whether the weakening would result in self-fertility would depend upon its selective value. If such self-fertility were undesirable to the species it could easily be eliminated by natural selection, either by reducing the threshold of the inhibition necessary to produce incompatibility or by increasing the amount of substrate the competition for which has led to the weakening.

A third type of interaction between **S**-alleles, would be the production in heterozygotes of a new antigen, distinct from that of the homozygotes. From our knowledge of gene action this would seem unlikely, but as such a situation has been considered by Lewis (1943*b*) and has been even postulated by Fernandes (1935) in *Narcissus triandrus*, it has been included for completeness.

Table 1 lists all possible combinations of gametophytic and sporophytic control with independence or dominance in pollen or style, but with the simplest background: one locus with two alleles. When there is dominance it is assumed to be of **S**₁ over **S**₂. There are three possible genotypes, represented for simplicity without the **S**'s as 11, 12 and 22, with 9 possible pollinations. All compatible pollinations are represented by a stroke, a heavy one when fully effective. When only one of the two kinds of gametes functions, this is shown by a suffix. When either of the compatible genotypes will be eliminated after one generation the stroke is crossed through. When the seed parent of a compatible cross-pollination is self-fertile it is assumed (except in E) that such a pollination is unimportant genetically and the stroke is broken. In case K the two compatible back-crosses together produce the same results as self-fertilisation so that even if they were frequent, they would have no effect on the frequencies of the three genotypes. Only in C would cross-fertilisation of the heterozygote produce a different result from the assumed complete self-fertilisation.

Three of the cases B, D and F are unworkable at the one locus two alleles level, for all compatible pollinations involve a genotype which could not exist for more than one generation. That this has no bearing on their practicability with more alleles is shown by the fact that B represents the *Nicotiana* type of incompatibility and F that frequently found in *Crepis* and *Parthenium*.

Let us now consider the workable cases individually. It is necessary to pause here to discuss gametophytic control on the female side, which does not seem to have been considered hitherto. If the embryo sacs secreted anti-bodies into the carpellar tissue and these diffused up the style the results would be indistinguishable from sporophytic control.

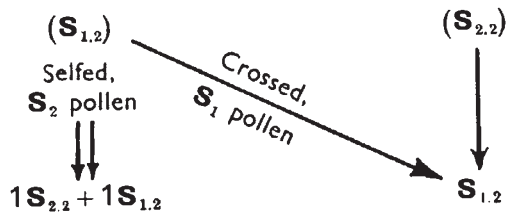
TABLE 1

POLLEN	CONTROL: INTERACTION:	G	G	G	S	POLLINATIONS											
						I	I	D	D	I	D	I	D	I	D	I	D
PISTIL	CONTROL: INTERACTION:	G	S	S	G	F	G	H	J	K	L	EQUILIBRIUM FREQUENCIES:					
CASE:	A	B	C	D	E	F	G	H	J	K	L	11	12	22			
$\left. \begin{matrix} 11 \\ 12 \\ 22 \end{matrix} \right\} \times 11$	•	•	•	•	•	•	•	•	•	•	•	•	•	•			
	X ₂	X	X	•	•	•	•	•	•	•	•	•	•	•			
	X	X	X	X	X	X	X	X	X	X	X	X	X	X			
$\left. \begin{matrix} 11 \\ 12 \\ 22 \end{matrix} \right\} \times 12$	X ₂	•	•	X ₂	X ₂	•	•	•	•	•	•	•	•	•			
	/	•	•	/	/	•	•	•	•	•	•	•	•	•			
	X ₁	•	•	X	X	•	•	•	•	•	•	•	•	•			
$\left. \begin{matrix} 11 \\ 12 \\ 22 \end{matrix} \right\} \times 22$	X	X	X	X	X	X	X	X	X	X	X	X	X	X			
	X ₁	•	•	/	/	•	•	•	•	•	•	•	•	•			
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		
												11	12	22			
												0.219	0.562	0.219			

Possible oppositional incompatibility systems with 1 locus and 2 alleles. At head of columns the letters *G* and *S* stand for gametophytic and sporophytic control. With sporophytic control there are four alternative interactions between two alleles in the heterozygous state: independence (*I*), dominance (*D*) of *S*₁ over *S*₂, natural weakening (*W*) and an entirely new action (*N*). The three genotypes are represented by the suffixes to the *S* symbol alone. For explanation of the body of the table see text.

It is just conceivable, however, that specific inhibitory substances could be secreted by ovules which had a very small radius of action. Growth of incompatible pollen tubes would be normal up to its inhibition at a point just prior to fertilisation. In this way, in *A* when $S_{1.2}$ was self-pollinated, S_1 pollen tubes would fertilise only S_2 embryo sacs and S_2 pollen tubes, only S_1 embryo sacs. In *A* there is only one compatible pollination at equilibrium, the self-fertilisation of the heterozygote. No self-incompatibility would be evident. The effect would correspond more to a balanced lethal system without loss of zygotes or to haplo-haploid incompatibility in fungi (Mather, 1944). Only the presence of further S -alleles, all with dominant marker genes closely linked to them, would allow the situation to be analysed. It can, however, be regarded as an outbreeding mechanism since it maintains heterozygosity at and near the S -locus.³

C. There are two genotypes at equilibrium, $S_{1.2}$ and $S_{2.2}$. $S_{1.2}$ is self-fertile with only half the pollen (S_2) functioning. $S_{2.2}$ is self-sterile but compatible with half the pollen (S_1) of $S_{1.2}$. If crossed as a pollen parent to $S_{1.2}$ it produces just the same as selfing $S_{1.2}$ but as the latter is self-fertile the pollen of $S_{2.2}$ will rarely function. The equilibrium position would be $2S_{1.2} : 1S_{2.2}$. Such a system could easily develop into gynodioecy by accumulation of recessive male-sterility genes near the S_2 locus. Similarly, deleterious recessives would rapidly accumulate at the S_1 locus which is never homozygous.



It will be seen that half the seed of the self-fertile will be self-sterile, but all the seed of the self-sterile will be self-fertile. After the development of male sterility, the $S_{1.2}$ hermaphrodites would produce half male steriles and the $S_{2.2}$ male steriles would produce only hermaphrodites.

Once male sterility had developed the self-incompatibility would become superfluous. If it disappeared the $S_{1.2}$ ♀ on selfing would produce ♂ and ♀ in the proportions between 3:1 and 2:1 according to the viability of $S_{1.1}$ and the ♀ would produce ♂ and ♀ in the proportion 1:1. This would alter the equilibrium frequencies however. If $S_{1.1}$ were inviable the equilibrium would become 3 : 2 (an increase in the frequency of ♀). If $S_{1.1}$ were fully viable the ♀ would be eliminated, as Lewis has shown (1941), and all trace of an outbreeding mechanism would have disappeared. Case C, with or without derived male sterility, would be just as effective an outbreeding mechanism as

male sterility derived independently of incompatibility. The possible evolution of C is shown below in chronological order:

1. Self-incompatibility with 2 alleles **S**₁ and **S**₂:

S₁ dominant over **S**₂ in style: gametophytic control of pollen.

Seed of **S**_{1.2} will be 1**S**_{1.2} : 1**S**_{2.2}.

Seed of **S**_{2.2} will be **S**_{1.2} only:

Equilibrium: 2**S**_{1.2} (self-fertile) : 1**S**_{2.2} (self-sterile).

2. Accumulation of recessive male sterility genes close to **S**₂:

Accumulation of deleterious recessives close to **S**₁.

Equilibrium (as in stage 1):

2**S**_{1.2} (self-fertile ♂) : 1**S**_{2.2}. (♀)

3. Breakdown of incompatibility reaction with **S**₁ acting as recessive lethal:

Seed of **S**_{1.2} will be 2**S**_{1.2} : 1**S**_{2.2}.

Seed of **S**_{2.2} will be 1**S**_{1.2} : 1**S**_{2.2}.

Equilibrium: 3**S**_{1.2} ♀ : 2**S**_{2.2} ♀.

Lewis' argument (*ibid.*) against the likelihood of naturally occurring recessive male sterility could be circumvented, therefore, if it arose via self-incompatibility of case C. Evidence for its origin in this way would be the lethality or low viability of homozygous hermaphrodites.

Cases D and E with the control of the pollen and style reversed yield situations corresponding closely to B and C.

D, like B, is unworkable with 2 alleles.

E, like C, has only two genotypes at equilibrium, the homozygous dominant being eliminated and the homozygous recessive having a frequency of one-third. A very unusual situation arises from the fact that the **S**₁ ovules of the heterozygote will reject all its pollen tubes which will be phenotypically **S**₁ owing to dominance. Consequently only the **S**₂ ovules will be fertilised on self-pollination (giving **S**_{1.2} and **S**_{2.2} seed in equal frequencies) and the **S**₁ ovules will remain available for **S**₂ pollen from the homozygotes. We thus have self-fertile plants in which with free access of pollinators, regularly half the seed will be self-fertilised and half cross-fertilised. The pollen of the homozygotes will thus have a function to perform and male sterility would be unlikely to arise.

We now consider those cases in which control is sporophytic in both style and pollen. As already stated, F is unworkable with only 2 alleles.

G has only one compatible pollination **S**_{1.2} × **S**_{2.2}. Thus neither the pollen of **S**_{1.2} nor the style of **S**_{2.2} is functioning. We have a hermaphrodite morphology but functional dioecy with **S**_{1.2} acting as female and **S**_{2.2} as male. Such a system would not be expected to function long without evolving into morphological dioecy by loss muta-

tion, the **S**-bearing chromosome acting as sex-chromosome and the females being heterogametic. Thus we see a possible path for the evolution of sex through incompatibility.

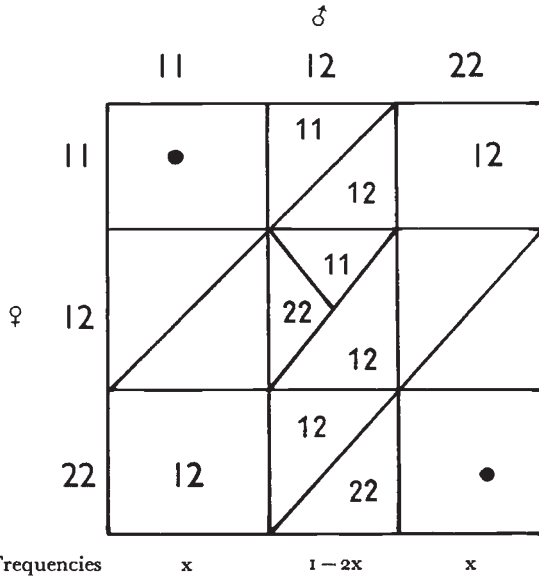
H. In just the same way and for the same reasons this would be expected to evolve into dioecy with heterogametic males.

J. Here there are two groups again but this time they are cross-compatible in either direction. As a breeding mechanism it is identical with the dipolar heterostyly of *Primula*. **S**₁ corresponds to **S** and **S**₂ to **s**. The heterostyly is, however, lacking. Since, however, half the pollinations would be incompatible there would be a large wastage of pollen which could be overcome by a morphological mechanism which reduced the chances of incompatible pollinations. Heterostyly as in *Primula* may be such a mechanism, though I am not aware that it has been proved experimentally. In which case selection might favour the evolution of heterostyly from such a homostyled incompatibility. On the other hand in *Armeria* and *Limonium* (Baker, 1948) the dimorphism is not of a kind likely to reduce the chances of illegitimate pollination. It might be directly related to the physiology of the incompatibility itself, whether oppositional or complementary.

K represents the weakening of both alleles in the heterozygous condition, in both style and sporophytically controlled pollen. One could have considered unilateral weakening in combination with dominance, independence and gametophytic control, but this would have led to unnecessary elaboration of the argument, since whether the weakening is in pollen, style or both, the main effect will be the same, namely, self-fertility of the heterozygote together with self-sterility of the homozygotes, leading to a continuous cycle from self-fertilisation to cross-fertilisation with each generation. Within a single population this provides a situation in which at the same time there will be much of both potential and free variability. The potential variability will reside in the plants produced by cross-fertilisation of the self-steriles. The free variability will arise by the self-fertilisation of the self-fertiles produced by cross-fertilisation. Such a breeding system might have special advantages when a rapid and large scale response to selection was required.

To consider K in detail. This is best done with the aid of the mating diagram opposite (symbols as in fig. 3).

The progenies obtained from each compatible mating are shown in the appropriate squares. At generation n the frequencies of **S**_{1.1} and **S**_{2.2} will be equal, say x . Then the frequency of **S**_{1.2} is $(1 - 2x)$. In calculating the equilibrium frequency it is assumed that all genotypes are equally viable and fully fertile whether self-fertile or self-sterile. The contribution of a genotype as seed parent to the next generation will, therefore, be in proportion to its frequency in the general population. Owing to cross-incompatibility, however, the contribution of a genotype as pollen parent to the progeny of any seed parent will be in proportion to its contribution to the pool of *compatible pollen*, which will not normally be the same as its frequency in the general population.



On these assumptions if x_{n+1} is the frequency of **S**_{1.1} at generation ($n + 1$)

$$x_{n+1} = x_n \cdot \frac{1}{2} \cdot \frac{1 - 2x_n}{1 - x_n} + (1 - 2x_n) \cdot \frac{1}{4}$$

$$= \frac{1 - x_n - 2x_n^2}{4(1 - x_n)}$$

At equilibrium $x_{n+1} = x_n$. This gives us a quadratic equation in x , of which the solutions are 2.28075 and 0.21925, of which only the second is real. Therefore the equilibrium frequencies are, for **S**_{1.1} and **S**_{2.2}, 0.219 and for **S**_{1.2}, 0.562. If we allow for cross-fertilisation of **S**_{1.2} by **S**_{1.1} and **S**_{2.2}, the two back-crosses together, being equally frequent, will yield the same genotype in the same ratios as **S**_{1.2} selfed. The equilibrium would, therefore, be unaffected by cross-fertilisation of the self-fertile plants.

L. This involves a rather hypothetical type of gene reaction. The heterozygote is supposed to produce a reaction of equal strength to either homozygote, but qualitatively distinct. The only reason for its inclusion is that it has been proposed by Fernandes (1935) to explain the inheritance of tristyliness in *Narcissus triandrus*. It is, however, of interest to students of population genetics since it represents an example of complete genotypically dissortative mating. Each genotype is compatible only with the other two genotypes. In spite, however, of the novel determination the equilibrium is exactly the same as in K with complete self-fertilisation of the heterozygotes, namely 0.219 for **S**_{1.1} and **S**_{2.2} and 0.562 for **S**_{1.2}.

Summarising the discussion of these eleven distinct cases involving an oppositionally determined self-incompatibility with two alleles at

one locus, only three, B, D and F are unworkable. The failure of these three is due to the presence of too few alleles. All the remainder are workable in that they are self-perpetuating. A is unrecognisable as self-incompatibility being fully self-fertile but is nevertheless an out-breeding mechanism in that it maintains hybridity at a given locus. To date no gametophytically controlled incompatibility on the female side has been discovered though there seems no *a priori* reason for ruling it out altogether. It would appear that the probability of finding A, D and E in nature is low. From theoretical considerations L must be regarded as improbable. Of the remainder, C and K have self-fertile heterozygotes. It has been argued above that the occurrence of a regular amount of self-fertilisation does not undermine self-incompatibility and may even supplement it, giving a resultant breeding mechanism with particularly rapid release of variability. There is, however, one reason against self-fertility in heterozygotes being very widespread. In doubled-up plants with *Nicotiana* type of incompatibility heterozygous pollen is not always self-fertile (*e.g. Oenothera*, Lewis, 1947). Only certain pairs of **S**-alleles would, therefore, be expected to show mutual weakening in heterozygous conditions. However, a certain amount of self-fertility is common in otherwise self-sterile species and much material for studies in self-incompatibility is consciously selected for absence in self-fertility. Whether or not self-fertility in heterozygotes is a systematic feature of any self-sterile species, some of the sporadic self-fertility so frequently encountered (in particular found by Kakizaki, 1930, in *Brassica*) may be attributable to this effect.

C, G, H and J produce conditions appropriate to the evolution of gynodioecy, sex and heterostyly. Except in the last named the original incompatibility may become submerged, leaving little, if any trace of the path along which the later condition was derived.

7. SEVERAL ALLELES

Having discussed the simplest possible situation (one locus with two alleles), it is necessary to pursue the matter further by considering the action of several alleles. The main effect naturally will be an increase in the number of cross-compatible groups. Consequently where two alleles were inadequate to give any cross-compatibility (B, D and F of table 1) the systems become workable.

B. Three alleles will provide three cross-compatible mating groups; **S**_{1.2}, **S**_{1.3} and **S**_{2.3}. The cross-compatibility within the population rises from zero to 2/3. This is, of course, the *Nicotiana* system. But in all species so far studied there has always been a large or very large number of **S**-alleles. Once a species had achieved several alleles the cross-compatibility would be so high that it is doubtful whether any further increase would be advantageous to the *species*. However, any new allele will always have an initial advantage over its predecessors, in the first place because if it arises in a pollen grain that grain will be com-

patible with its own style, and in the second place because until it reaches equilibrium it will always have a lower amount of cross-incompatibility to meet than the older alleles. It is a feature of this scheme that any one genotype can never arise as seed on a plant of the same genotype. This has a balancing effect tending to keep all genotypes equally frequent.

It may be noted in passing that this selection towards the equal frequency of all alleles and genotypes weakens Fisher's criticism (1947) of the author's estimates of the number of **S**-alleles in clover populations (Bateman, 1947). The criticism was that extreme variation in gene frequencies would cause under-estimation of the total number of alleles. Such extreme variation could only arise through mixing of populations or mutation and would be eliminated by natural selection.

D. The advent of a third allele would immediately produce a workable system as in B. New alleles would again be favoured by selection. One distinguishing feature between B and D is that in matings between plants with one common allele B will give a full seed set producing the paternal class plus a third, whereas D will give a 50 per cent seed set producing the maternal class plus a third.

F. Even three alleles does not give a workable system, for all homozygotes are eliminated at once and the three heterozygotes, **S**_{1.2}, **S**_{1.3} and **S**_{2.3} will be cross-incompatible since any pair has one common allele. With four alleles there will be six heterozygotes and each of these will be compatible only with one other, that with no common allele. Hence cross-compatibility within such a population would be only one sixth. It is doubtful whether fertility of the plants would be adequate for survival. With five alleles there is considerable improvement. There will be ten classes with cross-compatibility 3/10. Six alleles gives 15 classes with cross-compatibility of 2/5. Even this is lower than B or D with 3 alleles.

Thus under sporophytic control with independence of the alleles, the species could not survive with less than four alleles and the general fertility, depending on cross-compatibility, would be low even with more alleles. There would be strong selection favouring a large number of alleles, or, alternatively, non-independence. This suggests why *Parthenium* and *Crepis*, recently found to have completely sporophytic control, show considerable non-independence.

An interesting corollary to such a system is that since compatible pairs cannot have a common allele there is only one kind of family, falling into 4 classes with a cross-compatibility between sibs of one quarter. When there are only four alleles this is actually higher than the cross-compatibility in the entire population (one sixth). Under these circumstances *sib mating*, far from being discouraged by self-incompatibility, would actually be promoted.

Let us now consider those cases which already worked with two alleles.

A. As all heterozygotes are self-fertile and breed true, with three

alleles the population would consist of three independent lines whose frequencies would be independent also. Crossing two lines would produce an unusual result. With $\mathbf{S}_{1.2} \times \mathbf{S}_{1.3}$ the \mathbf{S}_1 ovules would be fertilised by \mathbf{S}_3 pollen only, whereas the \mathbf{S}_2 ovules would accept \mathbf{S}_1 and \mathbf{S}_3 . The progeny, therefore, would be $2\mathbf{S}_{1.3}$ (paternal) : $1\mathbf{S}_{1.2}$ (maternal) : $1\mathbf{S}_{2.3}$ (new genotype). None of these types would be distinguished by breeding behaviour since they are all self- and cross-fertile. The only possibility of recognising such a system would be by the recognition of dominant markers linked to the various \mathbf{S} -alleles.

L. The very special interaction between the \mathbf{S} -alleles in heterozygotes would make it appear even less likely that a third allele with a similar interaction with both the preceding ones could arise.

All the other cases involve dominance or weakening in heterozygotes. If, therefore, the number of alleles increases beyond two, the number of possible combinations and permutations of dominance, independence, or weakening between the different pairs of alleles becomes very numerous. Let us illustrate this by taking the two relations dominance and independence and making the arbitrary assumption that with three alleles \mathbf{S}_1 , \mathbf{S}_2 and \mathbf{S}_3 only dominance of a lower number over a higher can occur (this amounts to predetermining the symbols we may use for the three alleles). It also implies that if A is dominant over B and C, C cannot be dominant over A. If $>$ is used for dominance of left over right and $=$ for independence, then we may have:

$$\begin{aligned} &\mathbf{S}_1 > \mathbf{S}_2 > \mathbf{S}_3, \\ &\mathbf{S}_1 > \mathbf{S}_2 = \mathbf{S}_3, \\ &\mathbf{S}_1 = \mathbf{S}_2 > \mathbf{S}_3, \\ \text{or } &\mathbf{S}_1 = \mathbf{S}_2 = \mathbf{S}_3. \end{aligned}$$

It must also be recognised that the incidence of dominance in pollen and style can be largely independent (Gerstel, 1950, and Hughes and Babcock, 1950). There are, therefore, 16 possible combinations of pollen and style reaction excluding any account of weakening in heterozygotes. One of these includes complete independence as described above under F. This leaves 15 combinations of sporophytic control, which together with three with gametophytic control of pollen and three with similar control of ovules makes 21 combinations for us to consider. All would be expected to give slightly different equilibrium values for the various genotypes.

We shall, therefore, consider only five representative samples. We shall assume that dominance, if it occurs, is in the form $\mathbf{S}_1 > \mathbf{S}_2 > \mathbf{S}_3$ and that it may occur in the style only, with gametophytic control C, or independence G, in the pollen, in the pollen only, with embryosac control E, or independence H, in the style, or in both style and pollen J.

In all five systems only five genotypes are possible after one generation, as the homozygous top-dominant $\mathbf{S}_{1.1}$ is never produced by compatible matings. The mating behaviour of the five genotypes is

shown in fig. 3. The dotted squares represent incompatible matings. The squares with the diagonal stroke in C and E are compatible cross-pollinations involving self-fertile seed parents which are, therefore, deemed unimportant and, for simplicity, ignored. In E however, only half the ovules of the three self-fertile genotypes are able to be self-fertilised. The other half are available to be shared among pollens with which they are compatible. These pollinations are represented by an incomplete diagonal enclosing the progeny genotypes. The half-occupied squares in C represent half-compatible matings. In calculating the various types of progeny of **S**_{2.2} and **S**_{3.3} as seed parents, therefore, account must be taken of the fact that only half the pollen of some parents is functioning and the contribution of these plants is weighted by $\frac{1}{2}$. The progenies obtainable from each relevant compatible pollination are shown within the square. All genotypes from one mating are equally frequent.

It will be noticed that H can be derived from G merely by interchanging the rows and columns. The pollinations of H behave as their reciprocals in G. The equilibrium frequencies are not identical, however, because of the effects of pollen competition.

The frequencies of all five genotypes in any generation can be expressed in terms of their frequencies in the previous generation. These frequencies are represented by the letters *v* to *z*. By equating the values of *v* to *z* for consecutive generations, equations relating to the equilibrium frequencies can be obtained.

In only one case, J, has a solution been obtainable algebraically and then only with the assistance of Dr J. A. Nelder, of the Vegetable Research Station, Wellesbourne.

In all five cases, as previously determined, there is a stable equilibrium with two alleles. Introduction of the third allele causes immediate unbalance, but the new equilibrium is achieved only after many generations.

Let the frequencies of **S**_{1.2} **S**_{1.3} **S**_{2.2} **S**_{2.3} **S**_{3.3}
 be *v* *w* *x* *y* *z*

C. At equilibrium, $v=x=0$; $z=1/3$ and $w+y=2/3$ both *w* and *y* having any positive value between 0 and $2/3$. The third allele is in effect superfluous as there is no selective advantage in the persistence of either **S**_{1.2} (*w*) or **S**_{2.3} (*y*) provided one or other (they are both self-fertile) is available to pollinate the self-sterile **S**_{3.3}. The position is essentially the same as when there are only two alleles (see table 1). It will be noticed that the only invariable as well as the commonest allele is **S**₃, the bottom recessive, with a frequency of $2/3$. If the population consisted in the first place of **S**₁ and **S**₂ only, at equilibrium $v=1/3$, $x=2/3$.

It can be shown that

$$v_{n+1} + x_{n+1} = v_n + \left(\frac{v_n + w_n}{v_n + 2w_n + y_n + 2z_n} \right) x_n$$

The above coefficient of x_n will be less than unity unless w, y and z are all zero. These three items all involve \mathbf{S}_3 . Thus the introduction of the bottom recessive \mathbf{S}_3 to a population containing only \mathbf{S}_1 and \mathbf{S}_2 would lead eventually to the disappearance of $\mathbf{S}_{1.2}$ (v) and $\mathbf{S}_{2.2}$ (x) with the establishment of the equilibrium given above. With the elimination of $\mathbf{S}_{2.2}$ the pollen of $\mathbf{S}_{3.3}$ ceases to have a function, encouraging male sterility just as with 2 alleles. On the other hand the introduction of either \mathbf{S}_1 or \mathbf{S}_2 into a population consisting of the other two alleles would have very little effect.

E. As an example in population genetics this is even more fluid than C. There is no single equilibrium frequency. If any arbitrary values are given to v, w, x, y and z there is a gradual change to an equilibrium peculiar to that set of initial values, the gene frequencies $\mathbf{S}_1, \mathbf{S}_2$ and \mathbf{S}_3 being close to their initial frequencies. If, therefore, a third allele is introduced to the system which previously had only two it will not tend to spread as in most other mating systems discussed herein.

G. It will be seen from fig. 3 that the five genotypes fall into three mating groups when considered as seed parents, but all behave differently as pollen parents. The only way in which I was able to determine the equilibrium frequencies was arithmetically, by choosing several arbitrary initial frequencies of the five genotypes and calculating the values in successive generations until they all converged on a stable set of frequencies, the equilibrium. The values thus obtained, correct to four decimals were:

$$\left. \begin{array}{l} v=0.1217 \\ w=0.2787 \\ x=0.0202 \\ y=0.3573 \\ z=0.2221 \end{array} \right\} \text{giving the } \left\{ \begin{array}{l} \mathbf{S}_1=0.2002 \\ \mathbf{S}_2=0.2597 \\ \mathbf{S}_3=0.5401 \end{array} \right.$$

H presents a very similar situation to G. The genotypes fall into five mating groups as females but three as males. The equilibrium frequencies (calculated in the same way) are slightly different from G:

$$\left. \begin{array}{l} v=0.1722 \\ w=0.2822 \\ x=0.0359 \\ y=0.3274 \\ z=0.1823 \end{array} \right\} \text{giving the } \left\{ \begin{array}{l} \mathbf{S}_1=0.2272 \\ \mathbf{S}_2=0.2857 \\ \mathbf{S}_3=0.4871 \end{array} \right.$$

J represents a simpler situation than G or H. The compatibilities as seen in fig. 3 are symmetrical. The five genotypes fall in to the same 3 mating groups whether as males or females. The three mating groups are intra-sterile and inter-fertile: $(v+w)$ forms group A, $(x+y)$ forms group B and z forms group C. It can be shown that an equilibrium is

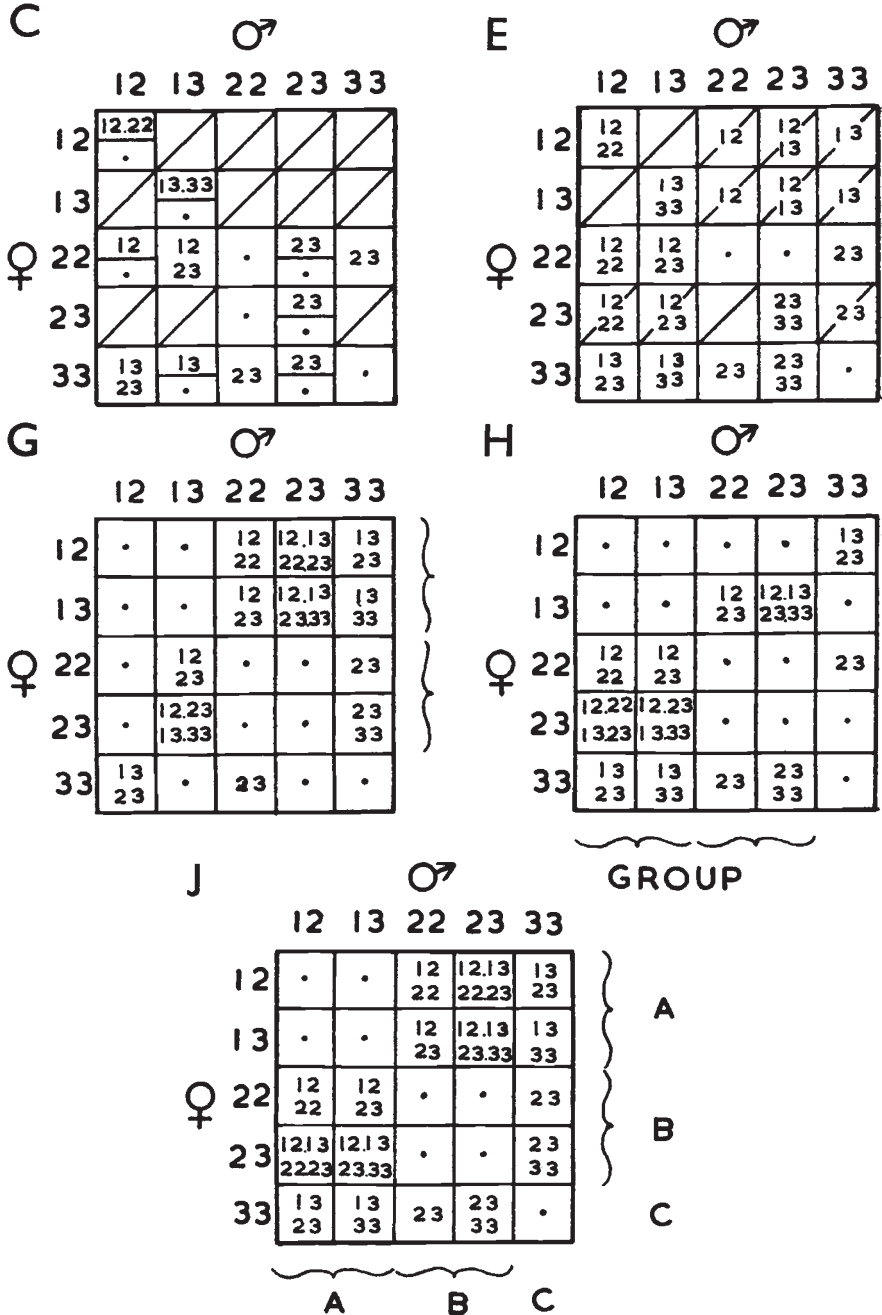


FIG. 3.—Possible matings in sample incompatibility systems with three alleles at one locus. There is sporophytic control accompanied by dominance on at least one side. When dominance occurs, the relationship is assumed to be $S_1 > S_2 > S_3$. The S-alleles are represented by their suffixes only. Incompatible pollinations have a dot in the square. Compatible cross-pollinations on to fully self-compatible seed parents have the square crossed through. In the remainder of the squares the progenies are represented. Where there is more than one genotype in a progeny, all are of equal frequencies. The cases (see table 1) are represented by the large letters. The half filled squares in (3) represent pollinations in which only half the pollen is compatible. The incomplete diagonals in (5) represent pollinations for which only half the ovules are available.

obtained if $A=B=C=1/3$ for which there is only one possible set of values:

$$\left. \begin{aligned} v &= \frac{2 - \sqrt{3}}{3} = 0.0893 \\ w &= \frac{\sqrt{3} - 1}{3} = 0.2440 \\ x &= \frac{7 - 4\sqrt{3}}{3} = 0.0239 \\ y &= \frac{4\sqrt{3} - 6}{3} = 0.3094 \\ z &= 1/3 = 0.3333 \end{aligned} \right\} \begin{array}{l} \text{giving gene} \\ \text{frequencies} \end{array} \left\{ \begin{array}{l} \mathbf{S}_1 = 0.1667 \\ \mathbf{S}_2 = 0.2233 \\ \mathbf{S}_3 = 0.6100 \end{array} \right.$$

For three alleles there appears to be only one possible equilibrium whatever the initial frequencies.

This scheme as represented in fig. 3 has a close empirical resemblance to Riley's hypothesis (1936) to explain the results in *Capsella grandiflora* though he postulated 2 loci with 2 alleles at each, with epistacy.

The resemblance extends even to the expected equilibrium frequencies, which would be the same as those calculated by Fisher (1949) for diploid trimorphic heterostyly as in *Oxalis*. Indeed, if the *S* and *M* loci of *Oxalis* were completely linked *MS* and *mS* chromosomes would be indistinguishable by any genetical tests and only the five genotypes given above (with those frequencies) could be recognised. Formally, one locus with three alleles showing serial dominance is the same as two completely linked loci each with two alleles showing dominance and the kind of epistacy peculiar to trimorphic heterostyly. But even without linkage between *M* and *S*, Fisher's estimates of *phenotype* frequencies are the same as those calculated above for the mating groups with three **S** alleles at one locus.

All five cases C, E, G, H and J have a common feature in favouring the bottom recessive **S**₃ and, where **S**_{1,2} heterozygotes are formed, the equilibrium frequency of the top dominant **S**₁ is least of the three. It may be assumed that with a multiple allelic series recessivity would always have a selective advantage.

Space does not permit a detailed consideration of the effects with 3 alleles of weakening in heterozygotes. There would presumably be the same predominance of the self-fertile heterozygotes.

Summarising the effects of increasing the number of alleles we can say that B, D and F produce fully workable systems though F needs a large number of alleles to achieve a favourable amount of compatible pollination. G, H and J remain functional but without the peculiar features present with only two alleles. They become more recognisable as typical incompatibility mechanisms with a single equilibrium. The alleles are not, however, of equal frequencies at equilibrium. The more recessive a particular allele, the higher its equilibrium frequency. A, C and E are less suited to polyallelic systems.

All gene frequencies are stable in A. There is an infinite series of equilibria in E, each corresponding to a different initial frequency. In C the homozygous bottom recessive has an equilibrium frequency of one third, the remainder of the population consisting of arbitrary amounts of the various self-fertile heterozygotes. K, with self-fertile heterozygotes through weakening of competing alleles, will be much the same with additional alleles. L becomes even more improbable.

8. SEVERAL LOCI

The effects of this variation have already been partly discussed in the section on the evolution of incompatibility. To some extent the effects of increasing the number of alleles and increasing the number of loci are opposite. An increased number of alleles increases cross-compatibility in the population but has little effect on sib compatibility. An increased number of loci *decreases* the cross-compatibility in the population and also between sibs. As will be seen in table 2 the cross-compatibility in the population as a whole is generally higher than

TABLE 2

Incompatibility Control	No. of Alleles	Sib Cross-compatibility <i>a</i>		General cross-compatibility <i>b</i>		Outbreeding Efficiency <i>b/a</i>	
		1 locus	2 loci	1 locus	2 loci	1 locus	2 loci
♂ Gametophytic: ♀ Sporophytic with independence Case B	3	0.25	0.063	0.33	0.11	1.33	1.78
	4	0.30	0.09	0.50	0.25	1.60	2.76
	∞	0.50	0.25	1.00	1.00	2.00	4.00
♂ and ♀ Sporophytic with independence Case F	4	0.25	0.063	0.167	0.028	0.67	0.44
	5	0.25	0.063	0.300	0.040	1.20	1.44
	∞	0.25	0.063	1.000	1.000	4.00	16.00
♂ and ♀ Sporophytic with dominance Case J	2	0.50	0.25	0.50	0.25	1.00	1.00
	3	0.52*	0.27	0.67	0.44	1.29	1.67
	∞	ca. 0.50	ca. 0.25	1.00	1.00	ca. 2.00	ca. 4.00

* This value obtained from Fisher's calculations (1949) for *Oxalis valdiviensis*

The effects of increasing the number of alleles and number of loci on cross-compatibility between sibs and amongst the general population from three types of incompatibility system.

among sibs. This ratio can be regarded as the outbreeding efficiency of a particular incompatibility system (the absence of self-fertilisation being a constant feature).

It must be stated here that since the incompatibility reaction is between pollen and style the degree of compatibility between plants should be expressed in terms of compatible pollen. With sporophytic control this is the same as the proportion of compatible plants. With gametophytic control of pollen such is not the case. Thus, both S_1S_3 and S_3S_4 plants are compatible as pollen parents with S_1S_2 but under open pollination (with pollen competition) pollen of S_1S_3 will

only be half as likely to effect fertilisation as pollen of S_3S_4 . Hence, in table 2, the cross-compatibility between sibs when there is gametophytic control and a large number of S -alleles is 0.5 and *not* 0.75 as stated by Fisher (1949). (Parent-offspring compatibility is also 0.5 and *not* 1.0.) This gives such a system a higher outbreeding efficiency than trimorphic heterostyly whether in respect of sib mating or parent-offspring mating. As shown earlier, trimorphic heterostyly resembles complete sporophytic control with three alleles at one locus showing dominance, which is entered in table 2.

An increase in number of loci from one to two, squares the frequencies of cross-compatibility. It thus squares the ratio of general to sib compatibility. Where, therefore, the outbreeding efficiency with one locus is greater than unity (as is usual) it is increased with two loci. When it is less than unity, in the special case of independent sporophytic control with one locus and four alleles, it is smaller still with two loci. With one locus and two alleles with dominance (as in dimorphic heterostyly), the outbreeding efficiency is unity. It remains so with two loci. Even when we consider only those instances in which increase in loci raises the outbreeding efficiency it is doubtful whether this effect would compensate the species for the general reduction of cross-compatibility, especially since, as argued earlier, the effect upon sib mating is unlikely to have a high selective value.

It is conceivable, however, that two loci could show interaction in the form of epistacy such that only one locus at a time was operating. The cross-compatibility could then remain high. Such a situation was proposed by Riley (1936) to explain his *Capsella grandiflora* data. The two loci were T, t and S, s with T epistatic to S.

9. SUMMARY

1. The possible range of self-incompatibility systems is derived *a priori*, and known systems are related to it.

2. These may act either by *promoting* the growth of pollen from genotypes *unlike* that of the style, or by *inhibiting* the growth of pollen from genotypes *like* that of the style. These are called complementary and oppositional mechanisms. Possible examples of both types are given. Oppositional mechanisms give the greatest evolutionary scope and are the most widespread.

3. Other classifications of incompatibility: hetero-*v.*, homomorphic, di- and tri-*v.* multipolar and haplo-diploid *v.* diplo-diploid are compared analytically.

4. Incompatibility has probably arisen *de novo* many times. Consequently all workable incompatibility systems are likely to be encountered in nature, and in all stages of development.

5. Self-incompatibility would probably evolve gradually, possibly from a condition of several weakly acting loci, by selection of modifiers to a condition where one or few main loci were active.

6. The workings of sporophytic control with independence, dominance or weakening in the interaction between alleles, of gametophytic control, and of varying numbers of alleles at one or more loci are discussed separately and in many combinations.

Acknowledgments.—The author wishes to acknowledge the assistance of Dr J. A. Nelder in estimating the equilibria on some of the incompatibility systems, and to express his appreciation of the helpful criticism of Dr D. Lewis with whom many of the arguments used herein have been discussed.

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Notes added in proof:

¹ Since writing the above Dr D. Lewis has published a paper (1952, Serological reactions of pollen incompatibility substances. *P.R.S.*, B, 140, 127-135), showing a serological resemblance between pollens with common S-alleles, bringing one stage nearer the demonstration that the incompatibility reaction does involve antigens.

² In a private communication Dr Å. Gustafsson claims to have found self-incompatibility in *Pinus sylvestris*, thus proving that the absence of a style does not prevent gymnosperms from evolving self-incompatibility.

³ Recent unpublished work by D. Wilkie of Glasgow has found in the pteridophyte *Pteridium aquilinum* a wholly gametophytic self-incompatibility quite analogous to case A, with a selective value much the same as in angiosperms. Thus the improbability of finding an example of case A in angiosperms is reduced.