INCOMPATIBILITY IN *COSMOS BIPINNATUS*

LESLIE K. CROWE

John Innes Horticulturol Institution, Hertford

Received 15.vi.53

I. INTRODUCTION

THE majority of self-incompatible plants in which the genetic basis of the mating system is known, belong to one of two classes. First there are the heteromorphic plants in which the genetic mechanism for outcrossing consists of one or two genes each with two alleles. There is dominance between the alleles in the pollen and in the style. The behaviour of the pollen is determined by the genotype of the mother plant, in other words by the sporophyte. *Primula* species are typical of this group. Secondly there are homomorphic plants in which there is one incompatibility gene with numerous alleles each acting individually in the pollen and in the style. The pollen behaviour is determined by the gametophyte. *Nicotiana*, *Oenothera* and *Trifolium* species are typical of this class.

Recent workers on *Parthenium argentatum* (Gerstel, 1950) and *Crepis fatida* (Hughes and Babcock, 1950) have described a novel type of incompatibility. To explain the results, one incompatibility gene is postulated with multiple alleles which act individually in the style as in *Nicotiana*, but the behaviour of the pollen is determined by the sporophyte and the alleles exhibit dominance, both features associated with the heteromorphic outbreeding types. Thus, for the first time a system has been described in two species of the Compositæ which combines genetic features typical of both the heteromorphic and homomorphic types of incompatibility. Regular features of this new system are reciprocal differences in compatibility, incompatibility between some F_1 plants and one or both parents, and plants which are homozygous for one allele.

There are two examples of this new breeding system in the Compositæ and it is therefore of interest to find out whether it is typical of the family as a whole. A report on incompatibility in *Cosmos bipinnatus* (Little, Kantor and Robinson, 1940) concluded that the mating system was similar in all respects to that of *Nicotiana*. The experiments, however, were not designed to show reciprocal differences in compatibility, or incompatibility between progeny and parents and these must be considered if the Composite type of system is to be distinguished from any other. This paper describes a reinvestigation of the mating behaviour of *C. bipinnatus*.

2. MATERIALS AND METHODS

Seed from open pollinated flowers of *C. bipinnatus* ($2n = 24$) was obtained from the Chelsea Physic Garden. Since this species is an annual, special measures were necessary to permit crossing between parents and their progeny. Firstly, by sowing seed as soon as it was ripe, the time lag due to dormancy was avoided. (Flowering started about twelve weeks after germination irrespective of the season.*) Secondly, parent plants were cut back regularly which prolonged their life until the progeny were in flower.

Pollinations for seed were made by dusting two heads together. Repeated self-pollinations on 12 plants failed to produce a single seed and consequently throughout the course of the work flowers were not emasculated. Compatible pollinations produce 20-30 seeds per head.

Compatibility was later determined solely by examination of pollen tube growth in the style. After pollination the heads were cut and transferred to an incubator running at 27°C . The styles were removed from the flowers 48 hrs. later, fixed in 1:3 acetic alcohol and stained in acid fuchsin and light green (Darlington and La Cour, 1947). Satisfactory staining takes 12-15 hrs. at 25°C . After an incompatible pollination the pollen grains germinate but the tubes seldom penetrate beyond the first layer of cells in the stigma and many are washed off in the process of fixing and staining. Compatible ones grow down well into the style.

The progeny from five crosses made on the original plants were studied in detail. Five parental plants were involved and these will be represented by the symbols P_I , P_{II} , P_{III} , P_{IV} and P_V . The crosses studied were (1) $P_I \times P_{II}$, (2) $P_{III} \times P_{IV}$, (3) $P_{IV} \times P_{III}$, (4) $P_{IV} \times P_V$ and (5) $P_V \times P_{IV}$. The results from the five crosses will be described in order, starting with $P_I \times P_{II}$.

3. RESULTS

Twelve plants of the progeny from the cross $P_I \times P_{II}$ were selfed and reciprocally intercrossed in all possible combinations. There were four mating groups which will be referred to as G_I , G_{II} , G_{III} and G_{IV} . The proportion of plants in each group was 5, 2, 3 and 2 respectively.

The plants within a group are all cross incompatible. As females, plants in G_I are compatible with G_{IV} only, while as pollen parents, G_I plants are compatible on G_{III} and G_{IV} stigmas but not with G_{II} . There is therefore a reciprocal difference in crosses involving plants in G_I and G_{III} . Group G_{II} is reciprocally compatible with G_{III} and G_{IV} which are themselves reciprocally compatible. The results are summarised in table 1.

All plants were reciprocally crossed with the two parents P_I and P_{II} . The results are given in table 2.

Plants in classes G_I and G_{II} are reciprocally incompatible with the female parent. With the male parent the same plants are compatible with the exception of the cross with G_I as female, which is incompatible. Classes G_{III} and G_{IV} are reciprocally compatible with the female parent but G_{IV} only is compatible with the male.

* *C. bipinnatus* is always classified as a "short day" plant. It is probable that, in captivity, selection has favoured plants with less rigid light requirements. Many horticultural varieties are now indifferent to day length in respect of flowering time. Recently a family of *Cosmos* segregated into plants which flowered in "long day" conditions and others which did not. The genetics of this difference is being investigated.

These results cannot be explained on the *Nicotiana* scheme proposed by East for, on this system, if the progeny from a cross fall into four groups, the groups are always cross compatible. In *Cosmos*, (i) the incompatibility between different mating types in the F_1 , (ii) incompatibility between parent plants and some of the offspring, and (iii) reciprocal differences in incompatibility are all features foreign

TABLE 1
*Incompatibility relations of 12 plants of the progeny
from the cross $P_1 \times P_{II}$*

$\begin{array}{c} \diagup \\ \text{♀} \end{array} \begin{array}{c} \text{♂} \end{array}$	G _I	G _{II}	G _{III}	G _{IV}
G _I	—	—	—	+
G _{II}	—	—	+	+
G _{III}	+	+	—	+
G _{IV}	+	+	+	—

— = incompatible.

+ = compatible.

to the *Nicotiana* system in which they occur only rarely and then as a result of illegitimate matings induced by special techniques such as bud pollination.

Turning to the Composite scheme proposed by Gerstel, Hughes and Babcock, again we find that although many of the results can be explained on this scheme it is not sufficient to account for all the data. By modifying this scheme, however, we can explain the facts.

TABLE 2
*Results of back-crossing the progeny of $P_1 \times P_{II}$
with the parents (reciprocally)*

F_1 groups	$P_1 \times F_1$	Reciprocal	$P_{II} \times F_1$	Reciprocal
G _I	—	—	+	—
G _{II}	—	—	+	+
G _{III}	+	+	—	—
G _{IV}	+	+	+	+

Let us follow Gerstel and postulate **R** as the incompatibility gene and the subscripts 3, 4, 5 and 6 as the alleles. (Alleles are allocated numbers which reflect their dominance relations, e.g. **R**₁ is dominant to **R**₂ and both are dominant to **R**₃.) Then the original cross can be represented **R**_{3,5} × **R**_{4,6} and the four classes in the progeny will be **R**_{3,4}, **R**_{3,6}, **R**_{4,5} and **R**_{5,6} respectively.

From the results we can deduce that the behaviour of the pollen of the first three types is determined sporophytically and that **R**₃

is dominant to the other three alleles and R_4 is dominant to R_5 and R_6 . To account for the behaviour of $R_{5,6}$ genotypes, a deviation from the scheme is necessary since the results can only be explained if the alleles R_5 and R_6 are under gametophytic control. In this respect, the system in *Cosmos* that we have suggested differs from *Parthenium* and *Crepis* in which pollen is always under sporophytic control.

It is possible to modify the Composite system in another way which would explain the facts equally well. If we assume that some alleles are dominant in the style as well as in the pollen and we represent the cross $P_I \times P_{II}$ as $R_{3,5} \times R_{4,5}$ then the four groups in the progeny would be $R_{3,4}$, $R_{3,5}$, $R_{4,5}$ and $R_{5,5}$ respectively. In this

TABLE 3

A comparison of the results of crossing Grv with P_I , P_{II} , G_{II} and G_{III} based on the two schemes discussed in the text

Cross	Gametophytic and sporophytic pollen determination		Dominance and individual action of alleles in the style	
	Genotype	Progeny expected	Genotype	Progeny expected
$P_I \times Grv$	$R_{3,5} \times R_{5,6}$	$R_{3,6}$; $R_{5,6}$	$R_{3,5} \times R_{5,5}$	$R_{3,5}$; $R_{5,5}$
Reciprocal	$R_{5,6} \times R_{3,5}$	$R_{3,5}$; $R_{3,6}$; $R_{5,5}$; $R_{5,6}$	$R_{5,5} \times R_{3,5}$	$R_{3,5}$; $R_{5,5}$
$P_{II} \times Grv$	$R_{4,6} \times R_{5,6}$	$R_{4,5}$; $R_{5,6}$	$R_{4,5} \times R_{5,5}$	$R_{4,5}$; $R_{5,5}$
Reciprocal	$R_{5,6} \times R_{4,6}$	$R_{4,5}$; $R_{4,6}$; $R_{5,6}$; $R_{6,6}$	$R_{5,5} \times R_{4,5}$	$R_{4,5}$; $R_{5,5}$
$G_{II} \times Grv$	$R_{3,6} \times R_{5,6}$	$R_{3,5}$; $R_{5,6}$	$R_{3,5} \times R_{5,5}$	$R_{3,5}$; $R_{5,5}$
Reciprocal	$R_{5,6} \times R_{3,6}$	$R_{3,5}$; $R_{3,6}$; $R_{5,6}$; $R_{6,6}$	$R_{5,5} \times R_{3,5}$	$R_{3,5}$; $R_{5,5}$
$G_{III} \times Grv$	$R_{4,5} \times R_{5,6}$	$R_{4,6}$; $R_{5,6}$	$R_{4,5} \times R_{5,5}$	$R_{4,5}$; $R_{5,5}$
Reciprocal	$R_{5,6} \times R_{4,5}$	$R_{4,5}$; $R_{4,6}$; $R_{5,5}$; $R_{5,6}$	$R_{5,5} \times R_{4,5}$	$R_{4,5}$; $R_{5,5}$

When alleles are dominant they are underlined

case the behaviour of the three alleles in the pollen must be sporophytically determined, R_3 being dominant to R_4 and R_5 , and R_4 dominant to R_5 . In the style R_3 and R_4 must be assumed to act individually when they occur together but both are dominant in combination with R_5 .*

The results expected on the alternative theories accord completely with those obtained.

It is possible to decide which of the two theories proposed is correct by reciprocally crossing plants of *Grv* with the parents and with plants of G_{II} and G_{III} since the results expected from these crosses are different on the two theories. Considering the first theory, *Grv*

* The evidence can also be interpreted on the basis that the parents are $R_{3,5}$ and $R_{4,6}$ and the pattern of dominance in the style is $R_3 \rightarrow R_5$ and $R_4 \rightarrow R_6$ and in the pollen is $R_3 \rightarrow R_4 \rightarrow R_5$. In the interests of brevity and clarity, only the simpler explanation involving 3 alleles is discussed in the text, since the principles involved are the same in both cases.

plants will be **R**_{5,6} and when they are crossed as females will give rise to progeny consisting of four mating groups, but as males only two groups will occur in the progeny. On the other hand, following the second theory when **G**_{IV} plants will be **R**_{5,5}, the same reciprocal crosses will produce only two mating groups in the progeny whichever way they are made, and furthermore the groups will be the same in the progeny from reciprocal crosses. Table 3 compares the results expected from these crosses in the case of each theory. It was not possible to make crosses between the female parent, **P**_I, and plants of **G**_{IV} because the **P**_I plant had stopped flowering, but all the other crosses were made and the progeny tested by intercrossing sibs in all possible combinations. The results are given in Table 4.

TABLE 4

*An analysis of the progeny from 6 test crosses between **G**_{IV} and the 3 plants **P**_{II}, **G**_{II} and **G**_{III}*

	P _{II}	R _{4,5}	G _{III}	R _{4,5}	G _{II}	R _{3,5}
G _{IV} ♀ R _{5,5}	G _V G _{IX}	7 6	G _{VI} G _X	6 5	G _{XIV} G _{XI}	5 4
G _{IV} ♂	G _{VII} G _{XII}	7 6	G _{VIII} G _{XIII}	7 6	Slightly self-compatible	

The numbers opposite the groups represent the number of plants in the group.

The progeny from each cross can be divided into two clear cut intra-sterile inter-fertile groups with one exception. The progeny from the cross **G**_{II} × **G**_{IV} were slightly self-compatible, producing 2 or 3 seeds per head after self-pollination. The reason for this is not certain but these plants had been in flower for some time before any pollinations were made on them and it is possible that the results were due to pseudo-fertility, reported by many workers to occur in self-incompatible plants towards the end of the season.

The results obtained are those anticipated on the theory that there is both individual action and dominance of alleles in the style depending on the combination of alleles present. They rule out the possibility of gametophytic pollen determination.

The two right hand columns in table 3 show that if the proposed scheme is correct, the genotype **R**_{5,5} should occur in the progeny of each cross and **R**_{4,5} in the progeny from the reciprocal crosses between **G**_{IV} and **P**_{II} and **G**_{IV} and **G**_{III}. **R**_{3,5} should occur in the progeny from crosses between **G**_{II} and **G**_{IV}. We already know the behaviour of these genotypes when they are intercrossed, therefore by selecting one plant from each of the two groups in the progeny of all six test crosses and intercrossing them we should get additional evidence in support of the proposed scheme. This was done: the self-fertile

plants from the cross $G_{II} \times G_{IV}$ being omitted. A plant in class G_I ($R_{3,4}$) was included in these crosses which should therefore include all four genotypes occurring in the progeny of the original cross $P_I \times P_{II}$. The results are recorded in table 5, and it will be seen that, as expected, the mating reactions form exactly the same pattern as that recorded in table 1.

Plants classified on the results as $R_{5,5}$ occur in the progeny of every test cross as expected and $R_{3,5}$ and $R_{4,5}$ types also occur in the progeny as forecast. Thus we have proof that the deviation from the composite type of mating system found in *Cosmos* amongst the

TABLE 5
The inter-relations of progeny obtained by crossing
 P_{II} , G_{II} , and G_{III} with G_{IV}

$\begin{array}{c} \text{♂} \\ \diagdown \\ \text{♀} \end{array}$	G_I	G_{XIV}	G_V-G_{VIII}	$G_{IX}-G_{XIII}$	
G_I	—	—	—	+	$R_{3,4}$ $R_{3,5}$ $R_{4,5}$ $R_{5,5}$
G_{XIV}	—	—	+	+	
G_V-G_{VIII}	+	+	—	+	
$G_{IX}-G_{XIII}$	+	+	+	—	
	$R_{3,4}$	$R_{3,5}$	$R_{4,5}$	$R_{5,5}$	$\begin{array}{c} \text{♀} \\ \diagdown \\ \text{♂} \end{array}$

progeny of the cross $P_I \times P_{II}$ can be attributed to dominance of alleles in the style.

* * * * *

Further evidence of dominance of alleles in the style was obtained from the progeny from reciprocal crosses between P_{III} and P_{IV} . Amongst 19 progeny from the cross $P_{III} \times P_{IV}$, 247 out of the possible 361 different pollinations were made with the result that 2 mating groups, G_{XV} and G_{XVI} were found in the proportion 10 : 9. All plants within each group were self and cross incompatible with one exception. Crosses between groups were compatible with 3 exceptions. Ten plants from the reciprocal cross $P_{IV} \times P_{III}$ were tested and again 2 intra-sterile inter-fertile types, G_{XVII} and G_{XVIII} , were found in equal numbers.

Such results by themselves could readily be explained on the *Nicotiana* type of mating system by supposing that the parent plants had one incompatibility allele in common. For example a cross such as $S_{1,2} \times S_{2,3}$ would give progeny of two genotypes $S_{1,3}$ and $S_{2,3}$ which when intercrossed would fall into two intra-sterile inter-fertile groups as was found in *Cosmos*. Similarly the reciprocal cross $S_{2,3} \times S_{1,2}$ would yield progeny with the genotypes $S_{1,2}$ and $S_{1,3}$.

In such a case the results of intercrossing the progeny from the reciprocal crosses and the results of crossing progeny and parents are predictable. One mating type in the progeny from each cross will be incompatible with the male parent and the other mating type will be common to both families. By making the appropriate crosses it was therefore a simple matter to show that such an explanation could not be applied to the families of *Cosmos* under discussion.

Results obtained in *Cosmos* which differ from those expected on the *Nicotiana* system are compared in table 6.

Gxvi and Gxvii plants are reciprocally incompatible in *Cosmos* but so too are plants in classes Gxv and Gxvii, which is not so in

TABLE 6

Comparison of the results expected from a semi-compatible cross in Nicotiana in which the parent plants have one allele in common and the results obtained in Cosmos

Cross	NICOTIANA Gametophytic pollen determination		COSMOS Sporophytic pollen determination
	Genotypes	Results expected	Results obtained
Piii × Piv	$S_{1,2} \times S_{2,3}$	+, 2 classes $\begin{cases} \text{Gxv } (S_{1,3}) \\ \text{Gxvi } (S_{2,3}) \end{cases}$	+, 2 classes $\begin{cases} \text{Gxv} \\ \text{Gxvi} \end{cases}$
Reciprocal	$S_{2,3} \times S_{1,2}$	+, 2 classes $\begin{cases} \text{Gxvii } (S_{1,2}) \\ \text{Gxviii } (S_{1,3}) \end{cases}$	+, 2 classes $\begin{cases} \text{Gxvii} \\ \text{Gxviii} \end{cases}$
Gxv × Gxvii	$S_{1,3} \times S_{1,2}$	+	—
Reciprocal	$S_{1,2} \times S_{1,3}$	+	—
Gxv × Piii	$S_{1,3} \times S_{1,2}$	+	+ and —
Piii × Gxvi	$S_{1,2} \times S_{2,3}$	+	+ and —
Piv × Gxv	$S_{2,3} \times S_{1,3}$	+	—
Piv × Gxvi	$S_{2,3} \times S_{2,3}$	—	+
Reciprocal	$S_{2,3} \times S_{2,3}$	—	+

Nicotiana. This suggests that whichever way the cross between the parents Piii and Piv is made the resulting progeny is the same.

The two crosses Gxv × Piii and Piii × Gxvi show that in *Cosmos*, plants within the same groups when classified according to their behaviour with sibs, do not all behave alike when crossed with their parents, again differing from the results based on the *Nicotiana* system, and proving that there must be two genotypes within one group.

On the Composite mating system we can designate Piii as R7,8 and Piv as R1,2. The progeny from the reciprocal crosses between these two types would be R1,7, R1,8, R2,7, and R2,8 in both cases. If we assume that R1 is dominant to R7 and R8 in the pollen then, despite the heterogeneity of plants carrying R1, they would all behave alike. Similarly if R2 is also dominant to R7 and R8 in the pollen, plants which are genotypically R2,7 and R2,8 would behave alike.

Consequently on intercrossing the four groups within a family only two mating reactions would be observed whichever way the parents were crossed and since the genotypes in the reciprocal progenies would be the same, intercrossing between them would again show the same two reactions. This is exactly the behaviour which was observed.

Progeny from the cross $P_{III} \times P_{IV}$ were intercrossed with the parents on a small scale only. The results are given in detail in table 7.

TABLE 7
Incompatibility relations between the parents P_{III} and P_{IV} and their progeny

$\begin{matrix} \nearrow \sigma \\ \searrow \text{♀} \end{matrix}$	Gxv		Gxvi		P_{III}	P_{IV}	
Gxv	—	—	<u>+</u>	<u>+</u>	—	+	$R_{1,7}$ $R_{1,8}$
Gxvi	<u>+</u>	<u>+</u>	—	—	<u>+</u>	<u>+</u>	$R_{2,7}$ $R_{2,8}$
P_{III}	<u>+</u>	<u>+</u>	<u>+</u>	<u>—</u>	<u>—</u>	<u>+</u>	$R_{7,8}$
P_{IV}	—	—	<u>+</u>	<u>+</u>	<u>+</u>	—	$R_{1,2}$
	$R_{1,7}$	$R_{1,8}$	$R_{2,7}$	$R_{2,8}$	$R_{7,8}$	$R_{1,2}$	$\begin{matrix} \searrow \text{♀} \\ \nearrow \sigma \end{matrix}$

Where alleles are known to be dominant they are underlined

If the genotypes $R_{1,7}$ and $R_{1,8}$ are allocated to Group XV we can decide arbitrarily which of these classes is incompatible with $R_{7,8}$ pollen and also which of the two classes $R_{2,7}$ and $R_{2,8}$ is incompatible on $R_{7,8}$ styles. The different behaviour of plants within a group in these crosses makes it possible to say with certainty that 14 of the 16 possible types of cross were made between the parents and the four incompatibility genotypes in the F_1 . The results of these pollinations do not give the complete picture of the dominance relations between the four alleles. They do show that, in the pollen, R_1 is dominant to the other 3 alleles, that R_2 is dominant to R_7 and that there is no dominance between R_2 and R_8 . In the style R_1 is dominant to R_2 and R_8 but there is individual action of alleles in $R_{1,7}$ styles. R_7 and R_8 must show individual action in the pollen or style or both, and R_2 is operative in $R_{2,8}$ and $R_{2,7}$ styles but we do not know whether or not it is dominant. This is the maximum amount of information we can extract from the evidence. Only the single pollination $R_{1,7}$ and $R_{1,2}$ gave a result at variance with these conclusions and this could be accounted for by an error when the cross was made.

Progeny from the reciprocal crosses between P_{IV} and P_V were intercrossed within the two families and in each case two intra-sterile,

inter-fertile mating classes only were observed. Crossing plants from the two different mating types in one family with those of the other gave exactly the same results as described in the case of $P_{III} \times P_{IV}$. Further tests were not made on these two families.

4. CONCLUSIONS

The breeding system in *Cosmos* is quite distinct from the *Nicotiana* system but closely resembles the type described in *Parthenium* and *Crepis*. Results can be explained on the basis of one incompatibility locus with multiple alleles. In the pollen the behaviour is determined sporophytically. In both the pollen and style the alleles show dominance or individual action according to the combination. The relation between the same alleles in the pollen and in the style sometimes varies.

FIG. 1.—Dominance relations of two groups of alleles in the pollen and style of *Cosmos*.

The interaction of different combinations of alleles in the pollen and in the style has been worked out. The dominance relations are summed up graphically in fig. 1.

5. DISCUSSION

The mating system in Cosmos in relation to other types

Parthenium and *Crepis* and all the types included in Class 6 (table 8) show the same genetic mechanism and all have individual gene action in the style. They are distinguished by the physiological behaviour of the pollen which is determined gametophytically in the *Oenothera* and *Nicotiana* types. But in *Parthenium* and *Crepis* the pollen control is sporophytic, some allele pairs showing dominance and others individual action. The pollen control of *Parthenium* and *Crepis* is

therefore akin to the heteromorphic class. In *Cosmos* the relationship is possibly even closer since not only is the pollen control similar, but in the style, too, dominance between alleles has been confirmed, so combining yet another character of the heteromorphic types with the genetic background of the *Nicotiana* group.

TABLE 8

A summary of the main types of self-incompatibility in plants and their mutual relations

	Species	Morphology	Gene mechanics	Gene physiology	
				Style	Pollen
1	<i>Primula</i> sp. <i>Linum grandiflorum</i>	Heteromorphic	1 gene, 2 alleles	Dominance	<i>Sporophytic control</i> Dominance
2	<i>Lythrum salicaria</i>	„	2 genes, 2 alleles	„	„
3	<i>Capsella grandiflora</i>	Homomorphic	„	„	„
4	<i>Cosmos bipinnatus</i>	„	1 gene, multiple alleles	Dominance and Individual action	„
5	<i>Parthenium argentatum</i> <i>Crepis fetida</i>	„	„	Individual action	Dominance and individual action
6	<i>Oenothera</i> sp. <i>Nicotiana</i> sp. <i>Trifolium</i> sp. <i>Prunus avium</i>	„	„	„	<i>Gametophytic control</i> Individual action

There is some evidence that in *Parthenium* too there may be dominance between alleles in the style. Gerstel does not mention this possibility but he found that $R_{4,4}$ pollen was compatible on $R_{1,4}$, $R_{2,4}$ and $R_{3,4}$ styles which can be explained if R_1 , R_2 and R_3 are dominant to R_4 in the style as he showed them to be in the pollen.

Dominance

In *C. bipinnatus* the dominance relations of alleles in the pollen sometimes present a picture of a linear series. For instance, R_3 is dominant to R_4 which is dominant to R_5 and R_3 is also dominant to R_5 . However, the whole series of alleles, which is probably extensive, does not conform to this simple pattern. There are already examples in *Cosmos*, *Crepis* and *Parthenium* of individual action of alleles in the pollen and if we consider the behaviour of some combinations

of alleles in the style of *Cosmos* we find a similar situation. Clearly therefore the linear pattern is subject to modification and it is not possible to predict the dominance relations of a pair of alleles. Furthermore their relations in the pollen and style are not necessarily the same. Complete reversal of the order of dominance in pollen and style has not been found and is unlikely since it would result in self-fertility.

6. SUMMARY

1. The progeny of three crosses with *Cosmos bipinnatus* all included 4 mating types.

2. Some groups within a family were cross-incompatible and there were reciprocal differences in this compatibility.

3. There was incompatibility between male and female parents and some of their progeny.

4. The results can be explained genetically by assuming that—

- (a) there is one incompatibility locus with multiple alleles,
- (b) the behaviour of the pollen is normally determined sporophytically and alleles exhibit dominance,
- (c) in the style alleles show dominance or individual action according to the combination.

5. The dominance relations between pairs of alleles cannot be predicted and may be different in the pollen and style.

6. The breeding system in this species conforms in general to the Composite type described in *Parthenium* and *Crepis*. But the dominance of some alleles in the style of *Cosmos* represents a still further combination of elements of the heteromorphic and homomorphic types of breeding system.

7. REFERENCES

- DARLINGTON, C. D., AND LA COUR, L. F. 1947. *The Handling of Chromosomes*. London : Allen & Unwin.
- GERSTEL, D. U. 1950. Self-incompatibility studies in Guayule. II. Inheritance. *Genetics*, 35, 482-506.
- HUGHES, M. B., AND BABCOCK, E. B. 1950. Self-incompatibility in *Crepis fetida* Subsp. *Rhoadifolia*. *Genetics*, 35, 570-588.
- LITTLE, T. M., KANTOR, J. H., AND ROBINSON, B. A. 1940. Incompatibility studies in *Cosmos bipinnatus*. *Genetics*, 25, 150-156.