A CASE OF MENDELIAN INHERITANCE COMPLICATED BY HETEROGAMETISM AND MUTATION IN *OENOTHERA* *PRATINCOLA*¹

FRIEDA COBB

University of Michigan, Ann Arbor, Michigan

Received June 21, 1920

TABLE OF CONTENTS

INTRODUCTION.....	1
Hypothesis of heterogametism.....	2
Equivalence, within strain C, of pollen of <i>Oenothera pratincola</i> f. <i>typica</i> and mut. <i>latifolia</i> ..	4
The F ₃ and F ₄ generations of the cross mut. <i>formosa</i> from strain E × mut. <i>latifolia</i> from strain C.....	5
The F ₁ and F ₂ generations of the cross f. <i>typica</i> strain C × mut. <i>formosa</i> strain E.....	6
The F ₁ and F ₂ generations of the cross mut. <i>formosa</i> strain E × f. <i>typica</i> strain E.....	7
The F ₁ and F ₂ generations of various crosses between f. <i>typica</i> M (the new Mendelian strain) and f. <i>typica</i> of strain C, f. <i>typica</i> of strain E, and mut. <i>formosa</i>	8
Various pedigrees of plants used in crosses.....	9
DISCUSSION.....	10
SUMMARY.....	13
LITERATURE CITED.....	15
APPENDIX—TABLES.....	15

INTRODUCTION

In the study of heredity in the genus *Oenothera* simple Mendelian results are very rarely obtained. It is generally conceded that the unusual results are due to the production, by a single morphologically uniform strain, of gametes of more than one type. The explanations have been various. The mutation hypothesis of DE VRIES is of course well known. It has not been generally accepted, however, as originally proposed. MORGAN (1918) and MULLER (1918) have suggested point mutation, followed by crossing over, an explanation suggested by their work on *Drosophila*. MULLER has worked out experimentally a balanced lethal stock of *Drosophila* in which certain seemingly aberrant phenomena of the *Oenotheras* find a parallel. To what extent the parallel affords an explanation we can not judge until the genetic analysis of the *Oenotheras* has been carried further.

¹ Papers from the Department of Botany of the UNIVERSITY OF MICHIGAN, No. 181.

The present paper is a contribution to the genetic analysis of *Oenothera pratincola*. It deals exhaustively with the first case in which simple Mendelian inheritance has been recognized and conclusively demonstrated when complicated by phenomena peculiar to the *Oenotheras*.

The strains of *Oenothera pratincola* used in this investigation were those of which the history has already been published (BARTLETT 1915 a, b; COBB and BARTLETT 1919). Although morphologically alike, one of them, designated as strain E, is genetically different from the other seven, of which strain C, the strain used in the experiments recorded in this paper, is a typical example.

Strain C produces in every generation a small number of mutations of several kinds (BARTLETT 1915 a). Some of these kinds appear also in strain E, but much more conspicuous in strain E are numerous mutations, of a strikingly distinct series, which do not occur in the other strains. These mutations occur in such numbers as to merit the term mass mutation (BARTLETT 1915 b) as a designation of the phenomenon. The series consists of four distinct types, all alike in having narrow, strongly revolute leaves, and in producing nothing but revolute-leaved plants in their progenies. Of these revolute-leaved mutations, mut. *formosa* (BARTLETT 1915 b), the strongest and most fertile of the series, was crossed with f. *typica* of strain E, and with strain C.

In a former paper (COBB and BARTLETT 1919) it has been stated that in reciprocal crosses between mut. *formosa* and f. *typica* E, from which mut. *formosa* arises, inheritance is matroclinic. Strain C pollinated by mut. *formosa* gives a matroclinic progeny; but the reciprocal cross, mut. *formosa* pollinated by strain C, gives in the F_1 generation only f. *typica*, in the F_2 generation a Mendelian segregation of 3 f. *typica*: 1 mut. *formosa*.

HYPOTHESIS OF HETEROGAMETISM

The hypothesis of heterogametism offered (COBB and BARTLETT 1919) in explanation of these phenomena, assumes that two types of gametes occur in *Oenothera pratincola*, α gametes (usually female) and β gametes (usually male), the α gametes carrying some factors not represented in the β gametes. Each zygote is formed by the union of an α and a β gamete, and so gets (except in rare cases of metacliny) the α determiners of its pistillate parent and the β determiners of its staminate parent. It, in turn, produces α (female) and β (male) gametes. In the case of a cross, the zygote is quite unaffected by the nature of the α of its staminate parent and the β of its pistillate parent.

Besides its characteristic α or β part, each gamete carries a group of factors common to both α and β gametes. The characteristic α and β portions of the gametes may consist of a single chromosome or of a group of chromosomes, but probably the latter, for very few characters have been found which are not connected with the α or β portions of the gametes. At reduction, α and β behave as units; that is, there is no interchange of factors or chromosomes between the characteristic α and β portions, each passing into the gametes (the α into the female, the β into the male) just as it entered the zygote from the parent. There is, however, the usual free segregation among the remainder of the chromosomes, each member of the homologous pairs accompanying with equal frequency the α and the β portions. Thus factors entering a zygote in the characteristic α or β chromosome (or chromosomes) occur in the α or β gametes, respectively, which it produces; but those factors which entered the zygote in the remaining, freely segregating group of chromosomes, occur as frequently in the α as in the β gametes produced. Characters whose factors belong to the α or to the β portion are inherited matroclinically or patroclinically, respectively; those whose factors belong to homologous and freely segregating chromosomes common to both α and β gametes are inherited in a Mendelian manner.

Mut. *formosa* arose from f. *typica* E by modification of a factor for flatness in the α portion of the α gamete, that is, by change of a factor which has no counterpart in the β portion of the β gamete. Change being in the α (female) gamete only, inheritance in crosses between mut. *formosa* and f. *typica* E is therefore matroclinal. If mut. *formosa* is used as the pistillate parent the α gamete received by the progeny is the mutated α of mut. *formosa* (designated hereafter as α'), and the progeny is therefore mut. *formosa*; if f. *typica* is used as the pistillate parent the α gamete received by the progeny is the normal α gamete of *Oenothera pratincola*, and the progeny is f. *typica*.

Strain C differs from strain E in having, in addition to the factor for flatness in the α portion of the α gamete, a freely segregating (Mendelian) factor for flatness (F) present in both α and β gametes, of which the recessive allelomorph (f) is carried by strain E. Thus the constitution of strain C is $\alpha\beta FF$, and the gametes which it produces are αF (female) and βF (male). The constitution of strain E is $\alpha\beta ff$, and the gametes which it produces are αf (female) and βf (male). The constitution of mut. *formosa* is $\alpha' \beta ff$, and the gametes which it produces are $\alpha' f$ (female) and βf (male). Therefore strain C ($\alpha\beta FF$) pollinated by mut. *formosa* ($\alpha' \beta ff$) gives a flat-leaved progeny ($\alpha\beta Ff$) which breeds true, for the α gamete

concerned in the cross is normal; but mut. *formosa* ($\alpha'\beta ff$) pollinated by strain C ($\alpha\beta FF$) gives a flat-leaved progeny ($\alpha'\beta Ff$) (flat-leaved, notwithstanding the mutated condition of α' , because of the presence of one Mendelian factor for flatness, inherited from the pistillate parent) which shows in the next generation a Mendelian segregation of flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) and revolute-leaved plants ($\alpha'\beta ff$). The α' gamete concerned in the cross has lost the factor for flatness, and so those F_2 individuals that are recessive for the Mendelian factors for flatness show the revoluteness determined by α' . This new synthetic f. *typica* ($\alpha'\beta FF$ or $\alpha'\beta Ff$), differing in genetic composition from both f. *typica* C and f. *typica* E, carrying the factor for revoluteness masked by at least one of the Mendelian pair of factors for flatness, will be called f. *typica* M (homozygous or heterozygous, as the case may be).

The hypothesis of the genetic constitution of the plants, and the results of crossing, may be stated in brief as follows:

Strain C,	$\alpha\beta FF$, flat, and, with respect to this character, immutable.
Strain E,	$\alpha\beta ff$, flat, mutable.
Mut. <i>formosa</i> ,	$\alpha'\beta ff$, revolute-leaved.
Strain E $\times$ <i>formosa</i> ,	$\alpha\beta ff$, flat, mutable.
<i>Formosa</i> $\times$ strain E,	$\alpha'\beta ff$ revolute, breeding true with respect to this character.
Strain C $\times$ <i>formosa</i> ,	$\alpha\beta Ff$ flat, segregating with respect to mutability.
(Strain C $\times$ <i>formosa</i>) F_2	$\left\{ \begin{array}{l} 1 \alpha\beta FF \text{ flat, immutable, breeding true.} \\ 2 \alpha\beta Ff \text{ flat, continuing the segregation of the } F_1 \text{ generation.} \\ 1 \alpha\beta ff \text{ flat, mutable, otherwise breeding true.} \end{array} \right.$
<i>Formosa</i> $\times$ strain C,	$\alpha'\beta Ff$ flat, segregating with respect to revoluteness.
(<i>Formosa</i> $\times$ strain C) F_2	$\left\{ \begin{array}{l} 1 \alpha'\beta FF \text{ flat, non-segregating.} \\ 2 \alpha'\beta Ff \text{ flat, continuing the segregation of the } F_1 \text{ generation.} \\ 1 \alpha'\beta ff \text{ revolute, breeding true.} \end{array} \right.$

EQUIVALENCE, WITHIN STRAIN C, OF POLLEN OF OENOTHERA PRATINCOLA
F. TYPICA AND MUT. LATIFOLIA

The former paper (COBB and BARTLETT 1919) gave data of the F_1 and F_2 generations of the cross mut. *formosa* E $\times$ mut. *latifolia* C. At the time the original crosses between mut. *formosa* and strain C were made,

the cross mut. *formosa* $\times$ f. *typica* C was unsuccessful. But the pollen of mut. *latifolia* had been shown to be equivalent to the pollen of the f. *typica* from which it arises (the mutation to *latifolia* being concerned with the α gamete, the β gamete remaining as in f. *typica*), and therefore, in order to have a more complete series of crosses to work upon, the cross mut. *formosa* $\times$ mut. *latifolia* from strain C was used in place of the missing cross, mut. *formosa* $\times$ f. *typica* C. The substitution has been justified by later work, recorded in tables 5 and 6 of the present paper, which give analyses of the F_1 and F_2 generations of the cross mut. *formosa* $\times$ f. *typica* C. This cross was successfully made three years after the original crosses upon which much of the work recorded here is based.

The F_1 generation (see table 5) consisted of 100 plants from six different crosses, all of them flat-leaved. The F_2 generation (see table 6) consisted of 3274 plants, 2399 flat-leaved and 875 revolute-leaved; that is, a ratio of 2.74:1, in sufficiently good accord with the 3:1 of the Mendelian monohybrid ratio. The cross mut. *formosa* $\times$ mut. *latifolia* C, as recorded in the previous paper, gave in the F_1 generation 209 plants, all of them flat-leaved, and in the F_2 generation from normal f. *typica* plants of the F_1 generation, 6392 plants, 4759 flat-leaved and 1633 revolute-leaved; that is, a ratio of 2.91:1. This shows that the results in the F_2 generation are the same whether mut. *formosa* is pollinated by f. *typica* C or by mut. *latifolia* C; and this, in connection with the previous evidence (COBB and BARTLETT 1919) of the equivalence of the pollen from the two sources, gives ample justification for the substitution of f. *typica* M descended from mut. *latifolia* instead of the identical form descended from f. *typica* C.

THE F_3 AND F_4 GENERATIONS OF THE CROSS MUT. *FORMOSA* FROM STRAIN E
 $\times$ MUT. *LATIFOLIA* FROM STRAIN C.

The F_3 and F_4 generations of the cross mut. *formosa* $\times$ mut. *latifolia* C show a continuance of the Mendelian behavior of the F_2 generation (COBB and BARTLETT 1919). Self-pollination of normal f. *typica* plants of the F_2 generation gave in the F_3 generation (see table 2) 22 progenies consisting entirely of flat-leaved plants, showing the presence of homozygous dominants ($\alpha'\beta FF$) in the F_2 generation, and 41 progenies in which there were both flat-leaved and revolute-leaved plants, showing the presence of heterozygous dominants ($\alpha'\beta Ff$) in the F_2 generation. The ratio 22 uniform cultures to 41 segregating cultures very closely approximates the expected ratio of 1 homozygous dominant to 2 heterozygous dominants in the F_2 generation. In the segregating progenies of the F_3 generation

the ratio of flat-leaved to revolute-leaved plants is 3.08:1, in very close agreement with the expected 3:1 of the Mendelian monohybrid segregation.

All progenies of fewer than 20 plants were omitted from table 2 as being unreliable. A very small culture of flat-leaved plants might, had it been larger, have included some revolute-leaved plants, and thus a heterozygous dominant of the F_2 generation might be recorded as homozygous. If these cultures were included in the table, the ratio of non-segregating to segregating progenies would become 33:56 instead of 22:41, and the ratio of flat-leaved to revolute-leaved plants in the segregating progenies would become 2.94:1 instead of 3.08:1.

Self-pollination of 16 plants of f. *typica* M ($\alpha'\beta FF$) belonging to the non-segregating cultures of the F_3 generation gave in the F_4 generation (see table 3) 1114 plants, all of them flat-leaved. From these plants an F_5 generation has been grown, consisting of 695 plants belonging to 7 progenies, no progeny consisting of fewer than 29 plants. All were flat-leaved. Self-pollination of 3 plants chosen at random among the f. *typica* plants of the segregating cultures of the F_3 generation gave in the F_4 generation (see table 4) 2 segregating progenies and 1 non-segregating, showing a continuance of the Mendelian splitting to the fourth filial generation. It seems unnecessary to carry the line further.

The behavior of the recessives, mut. *formosa* ($\alpha'\beta ff$), of the F_2 generation of the cross mut. *formosa* $\times$ mut. *latifolia* C. was also in accord with expectation. The F_3 generation consisted of 69 plants belonging to progenies of 4 mut. *formosa* plants of the F_2 generation. All were revolute-leaved, and the 62 grown to maturity all proved to be mut. *formosa*. Also, 2388 plants belonging to the F_3 progenies from mut. *formosa* plants of the F_2 generation, of the cross mut. *formosa* $\times$ CD hyb. *viscida* were all revolute-leaved. Hyb. *viscida* is the form resulting from the cross *Oenothera pratincola* f. *typica* C $\times$ *Oenothera numismatica* (BARTLETT 1915 a). It is like f. *typica* C in all respects, except that, in addition to the pubescence normally occurring on the flowers of *Oenothera pratincola*, it has the viscid pubescence of *Oenothera numismatica*.

THE F_1 AND F_2 GENERATIONS OF THE CROSS F. TYPICA, STRAIN C $\times$ MUT. FORMOSA, STRAIN E

The Mendelian behavior following the cross mut. *formosa* $\times$ strain C has been demonstrated at length. The reciprocal cross, f. *typica* C $\times$ mut. *formosa* ($\alpha\beta FF \times \alpha'\beta ff$), is just as Mendelian in its segregation of the free factors for flatness, but the Mendelian segregation of factors finds no

chance to express itself in the zygote because of the ever-present α factor for flatness inherited from the pistillate parent. The only way for a revolute-leaved plant to occur in the F_2 or following generations of the cross is by an independent mutation from α to α' in the presence of the recessive condition of the Mendelian factors for flatness. Only one-fourth of the plants of the F_2 generation, those with the constitution $\alpha\beta ff$, are capable of becoming revolute-leaved by mutation. Apparently there is nothing to hinder mutation from α to α' in strain C. But in pure strain C the change would not be indicated by outward sign, for the strain is homozygous for the Mendelian factors for flatness. That this change does sometimes occur is shown by the few revolute-leaved plants which occur in the F_2 generation of the cross f. *typica* C $\times$ mut. *formosa* (see table 8, and COBB and BARTLETT 1919, table 6). In table 8 there are 26 revolute-leaved plants in a total of 1654, or 16 per 1000. If the mutation to α' should take place in a plant of the F_1 generation ($\alpha\beta Ff$), a 3:1 ratio would occur in the F_2 generation. In the hope that this may sometime happen in the experiment garden, the cross f. *typica* C $\times$ mut. *formosa* has been repeated many times, and F_1 and F_2 progenies are being grown.

THE F_1 AND F_2 GENERATIONS OF THE CROSS MUT. FORMOSA STRAIN E $\times$ F.
TYPICA STRAIN E

In the cross mut. *formosa* $\times$ f. *typica* E ($\alpha'\beta ff \times \alpha\beta ff$) the mechanism for Mendelian inheritance operates just as certainly as in the corresponding cross with f. *typica* C, but the two parents happen to be alike in the Mendelian factors under consideration, both being pure recessives, so the only type of inheritance which manifests itself is matrocliny, depending on the difference in factorial composition of the characteristic portions of the α and β gametes. This cross has been repeated successfully nine times, giving 305 plants in the F_1 generation (see table 9) and 628 plants, from four plants of the F_1 generation, in the F_2 generation (see table 10). All of the plants of both generations were revolute-leaved. The inheritance here is matroclinic, in contrast with the Mendelian inheritance in the corresponding cross with strain C.

The reciprocal cross, f. *typica* E $\times$ mut. *formosa* ($\alpha\beta ff \times \alpha'\beta ff$), has not been successfully repeated since the publication (COBB and BARTLETT 1919) of the fact that this cross is also matroclinic, the number of revolute-leaved plants occurring in the progeny being no greater than might be expected from self-pollination of f. *typica* plants of strain E, the strain which regularly produces some revolute-leaved plants in every generation.

THE F_1 AND F_2 GENERATIONS OF VARIOUS CROSSES BETWEEN F. *typica* M
(THE NEW, MENDELIAN STRAIN) AND F. *typica* OF STRAIN C,
F. *typica* OF STRAIN E, AND MUT. *formosa*

The data recorded in this paper concerning the F_1 and F_2 generations of crosses of eighteen different kinds between f. *typica* M (the new Mendelian strain from the cross mut. *formosa* $\times$ strain C) as one parent, and f. *typica* C, f. *typica* E, or mut. *formosa*, as the other parent, confirm the hypotheses of non-equivalent gametes and the presence of a pair of independent Mendelian factors in *Oenothera pratincola*.

All f. *typica* M plants used in the crosses were self-pollinated to determine whether they were homozygous or heterozygous.

All of the flat-leaved types other than f. *typica* which occurred in the progenies of crosses are mutations regularly thrown by f. *typica* C, and some of them by f. *typica* E also. All of the revolute-leaved types which occurred, are regularly thrown by f. *typica* E and by mut. *formosa*.

The cross mut. *formosa* $\times$ f. *typica* M (homozygous) ($\alpha'\beta ff \times \alpha'\beta FF$) gave in the F_1 generation (see table 11) only flat-leaved plants ($\alpha'\beta Ff$), and in the F_2 generation (see table 12) a segregation of 3 flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) to 1 revolute-leaved plant ($\alpha'\beta ff$).

The reciprocal cross, f. *typica* M (homozygous) $\times$ mut. *formosa* ($\alpha'\beta FF \times \alpha'\beta ff$), gave the same results (see tables 13 and 14).

The cross mut. *formosa* $\times$ f. *typica* M (heterozygous) ($\alpha'\beta ff \times \alpha'\beta Ff$) gave in the F_1 generation (see table 15) progenies consisting of flat-leaved plants ($\alpha'\beta Ff$) and revolute-leaved plants ($\alpha'\beta ff$) in approximately equal numbers, and in the F_2 generation from flat-leaved plants (see table 16) a segregation of 3 flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) to 1 revolute-leaved plant ($\alpha'\beta ff$).

The reciprocal cross, f. *typica* M (heterozygous) $\times$ mut. *formosa* ($\alpha'\beta Ff \times \alpha'\beta ff$) gave the same results (see tables 17 and 18).

The cross f. *typica* E $\times$ f. *typica* M (homozygous) ($\alpha\beta ff \times \alpha'\beta FF$) gave in both the F_1 and the F_2 generations (see tables 19 and 20) only flat-leaved plants. It is known that the α of strain E frequently mutates to α' , and a few revolute-leaved plants would therefore be expected in the F_2 progenies, by a combination of α' and the recessive Mendelian factors. One-fourth of the plants of the F_2 generation, those with the constitution $\alpha\beta ff$, would be expected to become revolute-leaved by mutation with the frequency of mutation in pure strain E. But this did not occur. The only explanation that can be suggested is that because the germination percentage was much higher than was expected, the seedlings were very much crowded in

the seed-pans, and possibly revolute-leaved plants, which do not hold their own in a dense stand, died before the seedlings were counted off. This, however, does not seem likely, and the matter will be further investigated.

The reciprocal cross, f. *typica* M (homozygous) $\times$ f. *typica* E ($\alpha'\beta FF \times \alpha\beta ff$), gave in the F_1 generation (see table 21) only flat-leaved plants ($\alpha'\beta Ff$) and in the F_2 generation (see table 22) a segregation of 3 flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) to 1 revolute-leaved plant ($\alpha'\beta ff$).

The cross f. *typica* M (heterozygous) $\times$ f. *typica* E ($\alpha'\beta Ff \times \alpha\beta ff$) gave in the F_1 generation (see table 23) flat-leaved plants ($\alpha'\beta Ff$) and revolute-leaved plants ($\alpha'\beta ff$) in about equal numbers, and in the F_2 generation from flat-leaved plants (see table 24) a segregation of 3 flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) to 1 revolute-leaved plant ($\alpha'\beta ff$).

The reciprocal cross is missing from the series.

The cross f. *typica* M (homozygous) $\times$ f. *typica* C ($\alpha'\beta FF \times \alpha\beta FF$) gave in both the F_1 and F_2 generations (see tables 25 and 26) only flat-leaved plants ($\alpha'\beta FF$ in both generations).

The reciprocal cross is missing from the series.

The cross f. *typica* M (heterozygous) $\times$ f. *typica* C ($\alpha'\beta Ff \times \alpha\beta FF$) gave in the F_1 generation (see table 27) only flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) and in the F_2 generation (see table 28) 11 progenies consisting entirely of flat-leaved plants ($\alpha'\beta FF$) and 7 progenies showing a segregation of 3 flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) to 1 revolute-leaved plant ($\alpha'\beta ff$). The ratio 11:7 does not approach as closely as would be expected the ratio of one dominant factor to one recessive factor in the gametes of the heterozygous pistillate parent of the cross. In this table there seems to be a shortage both of segregating progenies and of revolute-leaved plants in the segregating progenies, indicating that the pistillate parent and its progeny produce either fewer or weaker gametes bearing the recessive factor.

The reciprocal cross is missing from the series.

A summary of tables 5 to 28, inclusive, is given as table 29.

VARIOUS PEDIGREES OF PLANTS USED IN CROSSES

A record of the parentage of all of the plants used in this work is given as table 1. All plants not otherwise designated were f. *typica*.

It may be noticed that, though different strains of *Oenothera pratincola* behave differently as to the mutations that they throw when self-pollinated, and in the way that they behave in crosses, all f. *typica* plants within a strain, no matter how complicated, by crossing or mutation, their pedi-

greens may be, act in the same way. For instance, an f. *typica* from mut. *grisella* from f. *typica* C behaves exactly as f. *typica* C with no mutations in its direct ancestry, at least during the period in which the strain has been carried in the garden.

It may also be noted that all plants of mut. *formosa* appear the same and behave the same genetically regardless of extraction. Those used in crosses were of five different types of extraction: (1) directly from f. *typica* E, by self-pollination; (2) from f. *typica* E, first by mutation to *angustifolia*, then to mut. *nitidissima* and finally to mut. *formosa*, all by self-pollination; (3) from the cross mut. *formosa* $\times$ f. *typica* E, by matroclinic inheritance; (4) from the cross mut. *formosa* $\times$ strain C, by segregation; (5) from crosses with both strain C and strain E, by segregation and matroclinic inheritance, e.g., (mut. *formosa* $\times$ mut. *latifolia* C)—mut. *formosa* $\times$ f. *typica* E)—mut. *formosa*.

In many thousand offspring, mut. *formosa* has produced nothing but revolute-leaved plants.

DISCUSSION

It may seem to those who are used to working with organisms in which clear Mendelian inheritance is the usual thing, that this case in *Oenothera pratincola* has been worked out with unnecessary elaboration. But several considerations should be borne in mind: first, that evident Mendelian inheritance is so rare in *Oenothera* that only two indisputable cases have been recorded, that of mut. *brevistylis* (DE VRIES 1901, p. 223; 1903, pp. 151-179, 429) and that of the dwarf mutation from mut. *gigas* (DE VRIES 1915 b) and that all instances deserve therefore to be thoroughly examined; second, that in this case the Mendelian inheritance is apparently modified by inheritance of another kind, working simultaneously with and independently of the Mendelian inheritance; and third, that the hypothesis of heterogametism put forth to explain this other type of inheritance needs further testing.

If the explanations offered here are correct, we have, in addition to Mendelian inheritance masked by heterogametism, mutation masked by Mendelian factors. That the α of strain C can undergo mutation to α' is shown by the presence of a few revolute-leaved plants in the F_2 generation of the cross f. *typica* C $\times$ mut. *formosa*. These plants derive their α from strain C, but have the dominant Mendelian factors which are present in strain C replaced by their recessive allelomorphs (see table 8). There seems no reason to doubt that this mutation in α occurs just as frequently in the presence of the Mendelian factors for flatness (i.e., in pure strain C)

as in their absence. If such is the case, Mendelian factors hide the mutation until a suitable cross occurs to remove the factors. This may have some bearing on the question whether crossing induces mutation; it may be that crossing merely makes possible an external expression, by removing concealing Mendelian factors, of changes which occurred long since in the germ-plasm and have been passed on from generation to generation giving no visible sign of their presence. In the same way a single mutation, the loss of one concealing factor, in a single chromosome, might bring to light a whole series of new forms. (The several revolute-leaved types that have occurred in the experiment garden can all be permanently concealed by the single pair of Mendelian factors for flatness.) This may explain in part the apparent periodicity of mutability. Perhaps the organism does not have increased tendency to change, but hoards actual changes until chance brings them to light, "gruppenweise," by the removal of inhibiting factors through a mutation.

Though the condition of the Mendelian factors in *Oenothera pratincola* strains other than strains C and E has not been investigated, it seems probable, since they have given no revolute-leaved plants, that the other six strains are homozygous with regard to the factor for flatness. If strain E is the only one of the eight strains carrying the recessive factors, it might seem likely that it arose from one of the other strains by loss of a dominant factor, and consequent Mendelian segregation, rather than that the reverse change took place, were it not for the fact that strain E has produced in the experiment garden a mutation (mut. *nitidissima*) which, as shown by its behavior in crosses with mut. *formosa*, is a homozygous dominant in regard to the Mendelian factors for flatness. Whether both dominant factors were present in the original plant of mut. *nitidissima* and its F_1 generation is a question which cannot be answered, but it is clear that they are now present in the strain as it is carried on in the garden.

That a pure dominant strain might arise from a pure recessive strain, or the reverse, leaving no heterozygous plants to tell the tale, seems possible, for the heterozygotes, as they appear in the experiment garden, tend to have poor and irregular leaf development as young rosettes, and might easily be eliminated by natural selection. The modification of a factor for flatness in a single chromosome of a homozygous dominant, or the reverse modification in a homozygous recessive, would then be the only change in the germ-plasm necessary to produce one homozygous strain from the other.

Some explanation should be made of the unusually low germination percentages occurring in the cultures recorded in this investigation. As the

character flatness vs. revoluteness is one which is evident in even very young seedlings, many sowings were made merely for the sake of recording the nature of the seedlings, and the seedlings were then discarded. In order to give all possible space and attention to the cultures intended for the summer garden at the time which is most favorable for planting, the sowings for seedling counts were made early and got out of the way. This meant that the seeds did not have as long a rest period as they apparently need before germination. Had they been planted a month or two later (in February and March instead of December and January) the percentages of germination would have been very much higher.

In problems connected with comparative fertility and sterility it is of course quite necessary to know that all viable seeds are forced to germinate. The method worked out by DE VRIES (1915 a) and applied by DAVIS (1915) for forcing germination to completion, is especially suited to such problems. It will also throw light on the types that may be lost through selective mortality and selective germination rate when less thorough methods are used. This information is most valuable. But that the low germination percentage has no significant effect on the results of the experiments recorded here is shown by table 30. Here the ratios of flat-leaved to revolute-leaved plants are assembled from all of those cultures in which the expected ratio is 3:1, and arranged according to the germination percentage. It will be seen that three-fourths of the cultures have a germination percentage under 25 percent. But it may also be seen that the average of the ratios of cultures in which the germination is from 50 to 81 percent is no nearer the expected 3:1 ratio than are the averages from cultures with poorer germination. Even when less than 5 percent of the seeds germinated, the average is as close to the theoretical ratio as is that of any one of the five cultures with a germination over 50 percent, or as the average of these five cultures.

That selective germination, in connection with the types with which this problem is concerned, occurs to any significant extent seems impossible. The only evidence of such selection is a slight excess of revolute-leaved individuals, especially noticeable when the germination is poorer. There are four tables which show in the total an excess of flat-leaved plants, ten which show an excess of revolute-leaved plants. In work with this species it has been noticed that when the percentage of germination is very low the percentage of mutations is very high (BARTLETT 1915 a). General observations lead to the conclusion that poor germination tends to bring the unusual types into prominence rather than to conceal them.

This paper records the case of a single unit character of the zygote, revoluteness, determined by a complicated set of phenomena: an allelomorphic pair of factors (F and f), the dominance and recessiveness of which produce no effect on the zygote except when the particular mutational change from α to α' has taken place; a mutation (α to α') occurring repeatedly, but concealed, as long as self-pollination continues, by the Mendelian factors FF , and Mendelian segregation concealed by matroclinic inheritance dependent on heterogametism (α and β gametes). It is hoped that the case may help to throw light upon the seemingly peculiar behavior of the *Oenotheras*.

SUMMARY

1. The male and female gametes of *Oenothera pratincola* are not alike. Each zygote is formed by the union of an α (female) gamete and a β (male) gamete (except in rare cases which it is needless to mention here) and has the constitution $\alpha\beta$. It, in turn, produces α (female) and β (male) gametes.

2. The α (female) gametes may undergo such mutation that, unless certain factors for flatness are present, the resulting plants are revolute-leaved. Such mutated gametes are designated α' .

3. The β (male) gametes have no such possibility of producing revolute-leaved plants.

4. Strain C carries in both male and female gametes, but not in the characteristic α and β portions of the gametes, a freely segregating factor for flatness (F), in the presence of which revoluteness can not occur, even though the mutation to α' has occurred. The constitution of f. *typica* strain C is $\alpha\beta FF$.

5. Strain E does not carry in either male or female gametes the independent factor for flatness which occurs in strain C, but its allelomorph (f). The constitution of f. *typica* strain E is $\alpha\beta ff$.

6. Mut. *formosa*, a revolute-leaved mutation thrown by strain E, differs from f. *typica* strain E in that it contains a mutated α (α'). The constitution of mut. *formosa* is $\alpha'\beta ff$.

7. There are two types of inheritance going on simultaneously and independently in *Oenothera pratincola*, matroclinic inheritance, connected with certain constant differences in factorial composition between male and female gametes, and Mendelian inheritance, connected with an independent segregation of factors carried by both gametes.

8. The cross mut. *formosa* $\times$ strain C ($\alpha'\beta ff \times \alpha\beta FF$) produces only flat-leaved plants in the F_1 generation; in the F_2 generation there occurs a Mendelian segregation in the ratio of 3 flat-leaved plants to 1 revolute

leaved plant. This segregation has been followed to the F_4 generation. The f. *typica* plants descended from this cross have the constitution $\alpha'\beta FF$ or $\alpha'\beta Ff$, and are called f. *typica* M (homozygous) and f. *typica* M (heterozygous), respectively.

9. The reciprocal cross, strain C $\times$ mut. *formosa* ($\alpha\beta FF \times \alpha'\beta ff$) also gives only flat-leaved plants in the F_1 generation; but in the F_2 generation there is no Mendelian segregation, though there occurs by mutation a small percentage (1.6 percent) of revolute-leaved plants. In this cross the inheritance appears to be matroclinic.

10. In reciprocal crosses between mut. *formosa* ($\alpha'\beta ff$) and f. *typica* E ($\alpha\beta ff$) the inheritance is purely matroclinic, as the two parents are alike in regard to the Mendelian factors for flatness.

11. The results, recorded in the tables of this paper, of various crosses between f. *typica* M and f. *typica* C, f. *typica* E and mut. *formosa* are all such as to favor the hypotheses of heterogametism and the presence of a pair of Mendelian factors for flatness in *Oenothera pratincola*. All the results obtained could be correctly predicted on the assumption that:

$$\begin{aligned} \text{f. } typica \text{ C} &= \alpha\beta FF \\ \text{f. } typica \text{ E} &= \alpha\beta ff \\ \text{mut. } formosa &= \alpha'\beta ff \end{aligned}$$

12. The α of strain C may become mutated to α' , but in pure strain C this change can find no expression, because of the Mendelian factors for flatness for which this strain is homozygous. That the change does sometimes occur here, as in strain E, is shown by the occurrence of a few revolute-leaved plants in the otherwise uniformly flat-leaved F_2 generation of the cross f. *typica* C $\times$ mut. *formosa*, plants in which the α portion of the constitution came from strain C and in which the Mendelian factors for flatness are replaced by their recessive allelomorphs from strain E.

13. The difference, with regard to Mendelian factors, between strains C and E is paralleled by the difference, with regard to the same factors, between mut. *nitidissima*, a type which has arisen in the experiment garden, and strain E from which it arose. Strain E is recessive; mut. *nitidissima* is a homozygous dominant. Evidently a homozygous dominant strain can arise from a homozygous recessive strain; the reverse process has not as yet been known to take place in the garden.

14. It is concluded that mutation may be masked by Mendelian factors, and that the apparent induction of mutation by hybridization may be merely the first appearance of changes which occurred in the past and

were carried on unseen until their appearance in the zygote was made possible by the removal, through hybridization, of inhibiting Mendelian factors.

LITERATURE CITED

- BARTLETT, H. H., 1915 a Additional evidence of mutation in *Oenothera*. Bot. Gaz. 59: 81-123.
 1915 b Mass mutation in *Oenothera pratincola*. Bot. Gaz. 60: 425-456.
 COBB, FRIEDA, and BARTLETT, H. H., 1919 On Mendelian inheritance in crosses between mass-mutating and non-mass-mutating strains of *Oenothera pratincola*. Jour. Washington Acad. Sci. 9: 462-483.
 DAVIS, B. M., 1915 A method of obtaining complete germination of seeds in *Oenothera* and of recording the residue of sterile seed-like structures. Proc. Nation. Acad. Sci. 1: 360-363.
 DE VRIES, HUGO, 1901, 1903 Die Mutations-Theorie. 2 vols., xii + 648 pp.; xiv + 752 pp. Leipzig: Veit & Co.
 1915 a The coefficient of mutation in *Oenothera biennis* L. Bot. Gaz. 59: 169-196.
 1915 b *Oenothera gigas nanella*, a Mendelian mutant. Bot. Gaz. 60: 337-345.
 MORGAN, T. H., 1918 Concerning the mutation theory. Sci. Monthly 6: 385-405.
 MULLER, H. J., 1918 Genetic variability, twin hybrids and constant hybrids, in a case of balanced lethal factors. Genetics 3: 422-499.

APPENDIX—TABLES

Explanations applying to all of the tables

In table 1, all plants not otherwise designated were f. *typica*.

F. *typica* M is the synthetic, Mendelian strain of *Oenothera pratincola* which arises from the cross mut. *formosa* × f. *typica* C (or other form with equivalent pollen).

The numbers in columns headed "Key number" refer to corresponding numbers in table 1. The numbers in columns headed "Parent plant" are the numbers of the individual plants in the progenies resulting from the crosses or self-pollinations recorded in table 1.

* indicates that the seeds sown were from a single capsule.

† indicates that seeds from two or more capsules were sown together.

All of the flat-leaved types mentioned in analyses of cultures are regularly thrown by self-pollinated f. *typica* C, and some of them also by f. *typica* E. All of the revolute-leaved types mentioned are regularly thrown by f. *typica* E and by mut. *formosa*.

Types other than f. *typica*, mut. *latifolia*, and mut. *formosa* mentioned in the following tables are:

Mut. *albicans* (BARTLETT 1915 b, page 449).

Mut. *angustifolia* (BARTLETT 1915 b, page 438).

Mut. *dimorpha*, an undescribed mutation.

Mut. *ericacea*, an undescribed mutation.

Mut. *fallax*, an undescribed mutation, as a seedling very much like mut. *nummularia*, and thrown by the same strains.

- Mut. *gigas* (BARTLETT 1915 b, page 443).
 Mut. *grisea*, an undescribed mutation.
 Mut. *grisella*, an undescribed mutation.
 Mut. *nitidissima* (BARTLETT 1915 b, page 440, table IV).
 Mut. *nummularia*, a mutation commonly thrown by strain C but never by pure strain E. (BARTLETT 1915 a, page 97; COBB and BARTLETT 1919.)
 Mut. *revoluta* (BARTLETT 1915 b, page 450).
 Mut. *setacea* (BARTLETT 1915 b, page 450).
 Mut. *sub-latifolia*, an undescribed mutation.
 Hyb. *viscida*, a hybrid of *Oenothera pratincola* × *Oenothera numismatica* (BARTLETT 1915 a, page 86). This form is like *Oe. pratincola* f. *typica* with the addition of the viscid pubescence of *Oe. numismatica*.

TABLE 1

Record of the parentage of all of the progenies recorded in the following tables with key numbers.
 All plants not otherwise designated are f. *typica*

1 ² E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>	}	4
×		
C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	}	190
×		
2 E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>	}	162
×		
3 C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	}	162 - 164 <i>formosa</i>
×		
4 E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>	}	162 - 153 <i>formosa</i>
×		
5 C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	}	162 - 30 <i>formosa</i>
×		
6 C - 52 - 6 <i>grisella</i> ³ - 31 <i>grisella</i> - 73 - 3	}	162 - 164 <i>formosa</i>
(= 3 No. 164 <i>formosa</i> × f. <i>typica</i> C)		
7 E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>	}	162 - 153 <i>formosa</i>
×		
8 C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	}	162 - 153 <i>formosa</i>
×		
9 C - 52 - 6 <i>grisella</i> - 31 <i>grisella</i> - 73 - 3	}	162 - 153 <i>formosa</i>
(= 3 No. 153 <i>formosa</i> × f. <i>typica</i> C)		
10 E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>	}	162 - 153 <i>formosa</i>
×		
11 C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	}	162 - 153 <i>formosa</i>
×		
12 C - 52 - 6 <i>grisella</i> - 31 <i>grisella</i> - 73 - 3	}	162 - 153 <i>formosa</i>
(= 3 No. 30 <i>formosa</i> × f. <i>typica</i> C)		

² These numbers are designated "key numbers" in subsequent tables.

³ An undescribed mutation.

TABLE 1 (continued)

7	E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i> × C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i> C - 52 - 6 <i>grisella</i> - 31 <i>grisella</i> - 73 - 3 (= 3 No. 138 <i>formosa</i> × f. <i>typica</i> C)	162 - 138 <i>formosa</i> ×
8	E - 5 - 199 <i>formosa</i> - 58 <i>formosa</i> - 15 <i>formosa</i> × C - 52 - 6 <i>grisella</i> - 25 - 1 - 41	
9	E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i> × C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i> E - 43 - 89 - 5 - 19 C - 22 - 7 - 40 - 5 - 9 - 2 (= 23 No. 2 <i>formosa</i> × f. <i>typica</i> C)	162 - 164 <i>formosa</i> × 2 <i>formosa</i> ×
10	C - 52 - 6 <i>grisella</i> - 25 - 1 - 43 - 2 E - 5 - 199 <i>formosa</i> - 58 <i>formosa</i> - 15 <i>formosa</i> × E - 43 - 89 - 5 - 1 (= f. <i>typica</i> C × 25 No. 63 <i>formosa</i>)	63 <i>formosa</i>
11	C - 52 - 6 <i>grisella</i> - 25 - 1 - 43 - 19 E - 5 - 199 <i>formosa</i> - 58 <i>formosa</i> - 14 <i>formosa</i> × E - 43 - 89 - 5 - 1 (= f. <i>typica</i> C × 25 No. 27 <i>formosa</i>)	27 <i>formosa</i>
12	C - 22 - 7 - 40 - 5 - 9 - 1 × E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i> - 62 <i>formosa</i>	27 <i>formosa</i>
13	C - 22 - 7 - 40 - 5 - 9 - 1 E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i> × C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i> E - 43 - 89 - 5 - 19 (= f. <i>typica</i> C × 23 No. 16 <i>formosa</i>)	162 - 164 <i>formosa</i> × 16 <i>formosa</i>
14	C - 52 - 6 <i>grisella</i> - 25 - 1 - 43 - 18 E - 5 - 199 <i>formosa</i> - 58 <i>formosa</i> - 15 <i>formosa</i> × E - 43 - 89 - 5 - 1 (= f. <i>typica</i> C × 25 No. 63 <i>formosa</i>)	63 <i>formosa</i>
15	C - 22 - 7 - 40 - 5 - 9 - 2 E - 5 - 199 <i>formosa</i> - 58 <i>formosa</i> - 15 <i>formosa</i> × E - 43 - 89 - 5 - 1 (= f. <i>typica</i> C × 25 No. 63 <i>formosa</i>)	63 <i>formosa</i>

TABLE 1 (continued)

16	$ \begin{array}{l} E - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \quad \times \\ C - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ \quad \quad \quad E - 43 - 89 - 5 - 19 \\ (= f. \textit{typica} C \times 23 \text{ No. 3 formosa}) \end{array} \left\{ \begin{array}{l} C - 22 - 7 - 40 - 5 - 9 - 2 \\ 162 - 164 \text{ formosa} \\ \times \\ 3 \text{ formosa} \end{array} \right\} $
17	$ \begin{array}{l} E - 5 - 199 \text{ formosa} - 58 \text{ formosa} - 35 \text{ formosa} \\ \quad \quad \quad \times \\ \quad \quad \quad E - 43 - 89 - 5 - 19 \end{array} \left\{ \begin{array}{l} \\ \\ \\ \end{array} \right\} $
18	$ \begin{array}{l} E - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \quad \times \\ C - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ \quad \quad \quad E - 43 - 72 - 5 - 6 \\ (= 3 \text{ No. 153 formosa} \times f. \textit{typica} E) \end{array} \left\{ \begin{array}{l} 162 - 153 \text{ formosa} \\ \times \\ \\ \end{array} \right\} $
19	$ \begin{array}{l} E - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \quad \times \\ C - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ \quad \quad \quad E - 43 - 72 - 5 - 6 \\ (= 3 \text{ No. 138 formosa} \times f. \textit{typica} E) \end{array} \left\{ \begin{array}{l} 162 - 138 \text{ formosa} \\ \times \\ \\ \end{array} \right\} $
20	$ \begin{array}{l} E - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \quad \times \\ C - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ \quad \quad \quad E - 43 - 72 - 5 - 6 \\ (= 3 \text{ No. 164 formosa} \times f. \textit{typica} E) \end{array} \left\{ \begin{array}{l} 162 - 164 \text{ formosa} \\ \times \\ \\ \end{array} \right\} $
21	$ \begin{array}{l} E - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \quad \times \\ C - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ \quad \quad \quad E - 43 - 89 - 5 - 1 \\ (= 3 \text{ No. 30 formosa} \times f. \textit{typica} E) \end{array} \left\{ \begin{array}{l} 162 - 30 \text{ formosa} \\ \times \\ \\ \end{array} \right\} $
22	$ \begin{array}{l} E - 5 - 199 \text{ formosa} - 58 \text{ formosa} - 14 \text{ formosa} \\ \quad \quad \quad \times \\ \quad \quad \quad E - 43 - 89 - 5 - 1 \end{array} \left\{ \begin{array}{l} \\ \\ \\ \end{array} \right\} $
23	$ \begin{array}{l} E - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \quad \times \\ C - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ \quad \quad \quad E - 43 - 89 - 5 - 19 \\ (= 3 \text{ No. 164 formosa} \times f. \textit{typica} E) \end{array} \left\{ \begin{array}{l} 162 - 164 \text{ formosa} \\ \times \\ \\ \end{array} \right\} $
24	$ \begin{array}{l} E - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \quad \times \\ C - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ \quad \quad \quad E - 43 - 89 - 5 - 19 \\ (= 1 \text{ No. 22 formosa} \times f. \textit{typica} E) \end{array} \left\{ \begin{array}{l} 4 - 22 \text{ formosa} \\ \times \\ \\ \end{array} \right\} $

TABLE 1 (continued)

25	E - 5 - 199 <i>formosa</i> - 58 <i>formosa</i> - 15 <i>formosa</i>		
	×		
	E - 43 - 89 - 5 - 1		
26	E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>		
	×		
	C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	162 - 138 <i>formosa</i>	
		×	
	E - 43 - 72 - 5 - 6		21 <i>formosa</i>
	E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>		×
	×		
	C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>		190 - 4 - 16
	(= 19 No. 21 <i>formosa</i> × 2 No. 4 - 16 f. <i>typica</i> M (homozygous))		
27	E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>		
	×		
	C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	162 - 138 <i>formosa</i>	
		×	
	E - 43 - 72 - 5 - 6		14 <i>formosa</i>
	E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>		×
	×		
	C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>		190 - 4 - 21
	(= 19 No. 14 <i>formosa</i> × 2 No. 4 - 21 f. <i>typica</i> M (homozygous))		
28	E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>		
	×		
	C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	162 - 153 <i>formosa</i>	
		×	
	E - 43 - 72 - 5 - 6		8 <i>formosa</i>
	E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>		×
	×		
	C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>		190 - 4 - 1
	(= 18 No. 8 <i>formosa</i> × 2 No. 4 - 1 f. <i>typica</i> M (homozygous))		
29	E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>		
	×		
	C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	162 - 153 <i>formosa</i>	
		×	
	E - 43 - 72 - 5 - 6		10 <i>formosa</i>
	E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>		×
	×		
	C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>		190 - 4 - 10
	(= 18 No. 10 <i>formosa</i> × 2 No. 4 - 10 f. <i>typica</i> M (homozygous))		
30	E - 5 - 199 <i>formosa</i> - 58 <i>formosa</i> - 15 <i>formosa</i>		
	×		
	E - 43 - 89 - 5 - 1		69 <i>formosa</i>
	E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>		×
	×		
	C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>		190 - 4 - 16
	(= 25 No. 69 <i>formosa</i> × 2 No. 4 - 16 f. <i>typica</i> M (homozygous))		

TABLE 1 (continued)

31	$ \begin{array}{l} \text{E - 5 - 199 } \textit{formosa} - 28 \textit{ formosa} \\ \times \\ \text{C - 22 - 13 } \textit{latifolia} - 87 \textit{ latifolia} \\ \text{E - 43 - 89 - 5 - 1} \\ \times \\ \text{E - 5 - 199 } \textit{formosa} - 28 \textit{ formosa} \\ \times \\ \text{C - 22 - 13 } \textit{latifolia} - 87 \textit{ latifolia} \end{array} \left\{ \begin{array}{l} 4 - 164b \\ \times \\ \times \\ \times \\ \times \\ \times \end{array} \right\} \begin{array}{l} 2 \textit{ formosa} \\ \\ \\ 190 - 54 - 6 \\ \\ \end{array} $
	(= 55 No. 2 <i>formosa</i> $\times$ 2 No. 54 - 6 f. <i>typica</i> M (homozygous))
32	$ \begin{array}{l} \text{E - 5 - 199 } \textit{formosa} - 28 \textit{ formosa} \\ \times \\ \text{C - 22 - 13 } \textit{latifolia} - 87 \textit{ latifolia} \\ \text{E - 5 - 199 } \textit{formosa} - 28 \textit{ formosa} \\ \times \\ \text{C - 22 - 13 } \textit{latifolia} - 87 \textit{ latifolia} \\ \text{E - 43 - 89 - 5 - 1} \end{array} \left\{ \begin{array}{l} 190 - 54 - 3 \\ \\ \times \\ 4 - 164b \\ \times \\ \times \end{array} \right\} \begin{array}{l} \\ \\ \\ 1 \textit{ formosa} \\ \\ \end{array} $
	(= 2 No. 54 - 3 f. <i>typica</i> M (homozygous) $\times$ 55 No. 1 <i>formosa</i>)
33	$ \begin{array}{l} \text{E - 5 - 199 } \textit{formosa} - 28 \textit{ formosa} \\ \times \\ \text{C - 22 - 13 } \textit{latifolia} - 87 \textit{ latifolia} \\ \text{E - 5 - 199 } \textit{formosa} - 28 \textit{ formosa} \\ \times \\ \text{C - 22 - 13 } \textit{latifolia} - 87 \textit{ latifolia} \\ \text{E - 43 - 89 - 5 - 1} \end{array} \left\{ \begin{array}{l} 190 - 54 - 6 \\ \\ \times \\ 4 - 164b \\ \times \\ \times \end{array} \right\} \begin{array}{l} \\ \\ \\ 1 \textit{ formosa} \\ \\ \end{array} $
	(= 2 No. 54 - 6 f. <i>typica</i> M (homozygous) $\times$ 55 No. 1 <i>formosa</i>)
34	$ \begin{array}{l} \text{E - 5 - 199 } \textit{formosa} - 28 \textit{ formosa} \\ \times \\ \text{C - 22 - 13 } \textit{latifolia} - 87 \textit{ latifolia} \\ \text{E - 5 - 199 } \textit{formosa} - 28 \textit{ formosa} \\ \times \\ \text{C - 22 - 13 } \textit{latifolia} - 87 \textit{ latifolia} \\ \text{E - 43 - 89 - 5 - 19} \end{array} \left\{ \begin{array}{l} 190 - 4 - 6 \\ \\ \times \\ 4 - 22 \textit{ formosa} \\ \times \\ \times \end{array} \right\} \begin{array}{l} \\ \\ \\ 13 \textit{ formosa} \\ \\ \end{array} $
	(= 2 No. 4 - 6 f. <i>typica</i> M (homozygous) $\times$ 24 No. 13 <i>formosa</i>)
35	$ \begin{array}{l} \text{E - 5 - 199 } \textit{formosa} - 28 \textit{ formosa} \\ \times \\ \text{C - 22 - 13 } \textit{latifolia} - 87 \textit{ latifolia} \\ \text{E - 5 - 199 } \textit{formosa} - 28 \textit{ formosa} \\ \times \\ \text{C - 22 - 13 } \textit{latifolia} - 87 \textit{ latifolia} \\ \text{E - 43 - 72 - 5 - 6} \end{array} \left\{ \begin{array}{l} 190 - 4 - 10 \\ \\ \times \\ 162 - 153 \textit{ formosa} \\ \times \\ \times \end{array} \right\} \begin{array}{l} \\ \\ \\ 10 \textit{ formosa} \\ \\ \end{array} $
	(= 2 No. 4 - 10 f. <i>typica</i> M (homozygous) $\times$ 18 No. 10 <i>formosa</i>)

TABLE 1 (continued)

36

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

162 - 153 *formosa*

×

E - 43 - 72 - 5 - 6

190 - 4 - 15

×

10 *formosa*

(= 2 No. 4 - 15 f. *typica* M (homozygous) × 18 No. 10 *formosa*)

37

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

162 - 153 *formosa*

×

E - 43 - 72 - 5 - 6

190 - 4 - 2

×

10 *formosa*

(= 2 No. 4 - 2 f. *typica* M (homozygous) × 18 No. 10 *formosa*)

38

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

162 - 153 *formosa*

×

E - 43 - 72 - 5 - 6

190 - 4 - 21

×

10 *formosa*

(= 2 No. 4 - 21 f. *typica* M (homozygous) × 18 No. 10 *formosa*)

39

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

162 - 30 *formosa*

×

E - 43 - 89 - 5 - 1

4 - 176 - 1

×

9 *formosa*

(= 1 No. 176 - 1 f. *typica* M (homozygous) × 21 No. 9 *formosa*)

40

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

162 - 30 *formosa*

×

E - 43 - 89 - 5 - 1

4 - 176 - 13

×

9 *formosa*

(= 1 No. 176 - 13 f. *typica* M (homozygous) × 21 No. 9 *formosa*)

41

E - 5 - 199 *formosa* - 28 *formosa* - 31 *formosa*

×

E - 5 - 199 *formosa* - 28 *formosa*

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

4 - 62

×

(= *formosa* × 1 No. 62 f. *typica* M (heterozygous))

TABLE 1 (continued)

42	$ \begin{array}{r} \text{E} - 5 - 199 \text{ formosa} - 58 \text{ formosa} - 15 \text{ formosa} \\ \times \\ \text{E} - 43 - 89 - 5 - 1 \\ \text{E} - 5 - 199 \text{ formosa} - 58 \text{ formosa} - 44 \text{ formosa} \\ \times \\ \text{CD} - 9 \text{ viscida}^4 - 26 \text{ viscida} - 11 \text{ viscida} - 24 \text{ viscida} \\ (= 25 \text{ No. 68 formosa} \times \text{viscida M (heterozygous)}) \end{array} $	$ \left. \begin{array}{c} 68 \text{ formosa} \\ \times \\ 6 \text{ viscida} \end{array} \right\} $
43	$ \begin{array}{r} \text{E} - 5 - 199 \text{ formosa} - 58 \text{ formosa} - 15 \text{ formosa} \\ \times \\ \text{E} - 43 - 89 - 5 - 1 \\ \text{E} - 5 - 199 \text{ formosa} - 58 \text{ formosa} - 12 \text{ formosa} \\ \times \\ \text{CD} - 9 \text{ viscida} - 26 \text{ viscida} - 11 \text{ viscida} - 24 \text{ viscida} \\ (= 25 \text{ No. 68 formosa} \times \text{viscida M (heterozygous)}) \end{array} $	$ \left. \begin{array}{c} 68 \text{ formosa} \\ \times \\ 1 \text{ viscida} \end{array} \right\} $
44	$ \begin{array}{r} \text{E} - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \times \\ \text{C} - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ \text{E} - 5 - 199 \text{ formosa} - 28 \text{ formosa} - 62 \text{ formosa} \\ (= 1 \text{ No. 165 f. typica M (heterozygous)} \times \text{formosa}) \end{array} $	$ \left. \begin{array}{c} 4 - 165 \\ \times \end{array} \right\} $
45	$ \begin{array}{r} \text{E} - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \times \\ \text{C} - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ \text{E} - 5 - 199 \text{ formosa} - 28 \text{ formosa} - 31 \text{ formosa} \\ (= 1 \text{ No. 164b f. typica M (heterozygous)} \times \text{formosa}) \end{array} $	$ \left. \begin{array}{c} 4 - 164b \\ \times \end{array} \right\} $
46	$ \begin{array}{r} \text{E} - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \times \\ \text{C} - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ \text{E} - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \times \\ \text{C} - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ (= 1 \text{ No. 163b f. typica M (heterozygous)} \times 1 \text{ No. 33 formosa}) \end{array} $	$ \left. \begin{array}{c} 4 - 163b \\ \times \\ 4 - 33 \text{ formosa} \end{array} \right\} $
47	$ \begin{array}{r} \text{E} - 43 - 89 - 5 - 1 - 2 \\ \text{E} - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \times \\ \text{C} - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ (= \text{f. typica E} \times 2 \text{ No. 4} - 2 \text{ f. typica M (homozygous)}) \end{array} $	$ \left. \begin{array}{c} \times \\ 190 - 4 - 2 \end{array} \right\} $
48	$ \begin{array}{r} \text{E} - 5 - 199 \text{ formosa} - 28 \text{ formosa} \\ \times \\ \text{C} - 22 - 13 \text{ latifolia} - 87 \text{ latifolia} \\ \text{E} - 43 - 74 - 41 - 45 - 2 \\ (= 1 \text{ No. 64} - 9 \text{ f. typica M (homozygous)} \times \text{f. typica E}) \end{array} $	$ \left. \begin{array}{c} 4 - 64 - 9 \\ \times \end{array} \right\} $

⁴ A hybrid of *Oenothera pratincola* $\times$ *Oe. numismatica* (BARTLETT 1915 a, p. 86). This form is like *Oe. pratincola* f. *typica* with the addition of the viscid pubescence of *Oe. numismatica*.

TABLE 1 (continued)

49

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 43 - 74 - 21 - 3

190 - 4 - 6

×

(= 2 No. 4 - 6 f. *typica* M (homozygous) × f. *typica* E)

50

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 43 - 72 - 5 - 6 - 12

190 - 54 - 2

×

(= 2 No. 54 - 2 f. *typica* M (homozygous) × f. *typica* E)

51

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 43 - 89 - 5 - 1 - 6

190 - 4 - 2

×

(= 2 No. 4 - 2 f. *typica* M (homozygous) × f. *typica* E)

52

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 43 - 74 - 21 - 3

4 - 176 - 1

×

(= 1 No. 176 - 1 f. *typica* M (homozygous) × f. *typica* E)

53

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 43 - 72 - 5 - 6

4 - 176

×

(= 1 No. 176 f. *typica* M (homozygous) × f. *typica* E)

54

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 43 - 89 - 5 - 1

4 - 165

×

(= 1 No. 165 f. *typica* M (heterozygous) × f. *typica* E)

55

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 43 - 89 - 5 - 1

4 - 164b

×

(= 1 No. 164b f. *typica* M (heterozygous) × f. *typica* E)

56

E - 5 - 199 *formosa* - 28 *formosa*

×

C - 22 - 13 *latifolia* - 87 *latifolia*

E - 43 - 89 - 5 - 1

4 - 163b

×

(= 1 No. 163b f. *typica* M (heterozygous) × f. *typica* E)

TABLE 1 (continued)

-
- 57 E - 5 - 199 *formosa* - 28 *formosa* }
 × } 4 - 167b }
 C - 22 - 13 *latifolia* - 87 *latifolia* } × }
 E - 43 - 89 - 5 - 19 }
 (= 1 No. 167b f. *typica* M (heterozygous) × f. *typica* E)
- 58 E - 5 - 199 *formosa* - 28 *formosa* }
 × } 190 - 4 - 6 }
 C - 22 - 13 *latifolia* - 87 *latifolia* } × }
 C - 52 - 6 - 25 - 1 - 43 - 2 }
 (= 2 No. 4 - 6 f. *typica* M (homozygous) × f. *typica* C)
- 59 E - 5 - 199 *formosa* - 28 *formosa* }
 × } 4 - 176 }
 C - 22 - 13 *latifolia* - 87 *latifolia* } × }
 C - 22 - 7 - 40 - 5 - 2 }
 (= 1 No. 176 f. *typica* M (homozygous) × f. *typica* C)
- 60 E - 5 - 199 *formosa* - 28 *formosa* }
 × } 4 - 167b }
 C - 22 - 13 *latifolia* - 87 *latifolia* } × }
 C - 22 - 7 - 40 - 5 - 2 }
 (= 1 No. 167b f. *typica* M (heterozygous) × f. *typica* C)
- 61 E - 5 - 199 *formosa* - 28 *formosa* }
 × } 4 - 165 }
 C - 22 - 13 *latifolia* - 87 *latifolia* } × }
 C - 22 - 7 - 40 - 5 - 2 }
 (= 1 No. 165 f. *typica* M (heterozygous) × f. *typica* C)
- 62 E - 5 - 199 *formosa* - 28 *formosa* }
 × } 4 - 163b }
 C - 22 - 13 *latifolia* - 87 *latifolia* } × }
 C - 22 - 7 - 40 - 5 - 2 }
 (= 1 No. 163b f. *typica* M (heterozygous) × f. *typica* C)
- 63 E - 5 - 199 *formosa* - 28 *formosa* }
 × } 4 - 186 *formosa* }
 C - 22 - 13 *latifolia* - 87 *latifolia* } × }
 E - 5 - 199 *formosa* - 28 *formosa* } × }
 × } 4 - 166 }
 C - 22 - 13 *latifolia* - 87 *latifolia* }
 (= 1 No. 186 *formosa* × 1 No. 166 f. *typica* M (homozygous))
- 64 E - 5 - 199 *formosa* - 58 *formosa* - 15 *formosa* }
 × } 69 *formosa* }
 E - 43 - 89 - 5 - 1 } × }
 E - 5 - 199 *formosa* - 28 *formosa* } × }
 × } 190 - 4 - 16 }
 C - 22 - 13 *latifolia* - 87 *latifolia* }
 (= 25 No. 69 *formosa* × 2 No. 4 - 16 f. *typica* M (homozygous))
-

TABLE 1 (concluded)

65

E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>	}	190 - 4 - 16
×		
C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	}	162 - 153 <i>formosa</i>
×		
E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>	}	x <i>formosa</i>
×		
C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	}	E - 43 - 72 - 5 - 6
×		
(= 2 No. 4 - 16 f. <i>typica</i> M (homozygous) × 18 No. x <i>formosa</i>)		

66

E - 5 - 199 <i>formosa</i> - 28 <i>formosa</i>	}	4 - 176
×		
C - 22 - 13 <i>latifolia</i> - 87 <i>latifolia</i>	}	×
×		
E - 5 - 208 <i>angustifolia</i> - 1 <i>nitidissima</i> ⁵ - 15 <i>formosa</i>	}	
×		
(= 1 No. 176 f. <i>typica</i> M (homozygous) × <i>formosa</i>)		

⁵ See BARTLETT 1915b, p. 440, table IV.

TABLE 2

A classification of the F₂ generation resulting from self-pollination of normal f. typica plants chosen at random from the segregating F₂ generation of the cross mut. formosa × mut. latifolia C. (Male gametes of mut. latifolia are the same as those of f. typica of the strain from which it arose).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE- LEAVED	RATIO
1	No. 16	370	57	42	15	2.80:1
1	No. 19	319	70	64	6	10.67:1
1	No. 20	598	22	19	3	6.33:1
1	No. 24	492	140	112	28	4.00:1
1	No. 26	448	57	45	12	3.75:1
1	No. 28	543	40	30	10	3.00:1
1	No. 29	578	78	62	16	3.88:1
1	No. 32	514	44	36	8	4.50:1
1	No. 37	243	62	42	20	2.10:1
1	No. 43	368	98	77	21	3.67:1
1	No. 44	299	62	53	9	5.89:1
1	No. 47	433	132	99	33	3.00:1
1	No. 62	209	162	125	37	3.38:1
1	No. 154a	227	56	38	18	2.11:1
1	No. 155a	316	63	40	23	1.74:1
1	No. 156	173	43	32	11	2.91:1
1	No. 158	278	104	84	20	4.20:1
1	No. 161	589	99	74	25	2.96:1
1	No. 163b	1,300	48	39	9	4.33:1
1	No. 164b	1,358	229	172	57	3.02:1
1	No. 167a	230	47	39	8	4.88:1
1	No. 167b	2,383	246	203	43	4.72:1
1	No. 168	598	129	95	34	2.80:1
1	No. 171	270	108	77	31	2.48:1
1	No. 175	518	123	93	30	3.10:1
1	No. 177a	178	42	32	10	3.20:1
2	No. 8	255	24	22	2	11.00:1
2	No. 9	338	35	26	9	2.89:1
2	No. 16	517	27	22	5	4.40:1
2	No. 18	506	23	15	8	1.87:1
2	No. 64	545	58	38	20	1.90:1
2	No. 65	562	107	73	34	2.15:1
2	No. 70	334	23	17	6	2.83:1
2	No. 73	567	161	105	56	1.87:1
3	No. 38	350	52	37	15	2.47:1
3	No. 72	472	55	46	9	5.11:1
3	No. 170	343	85	61	24	2.54:1
3	No. 183	491	33	20	13	1.54:1
3	No. 190	455	54	33	21	1.57:1
3	No. 198	215	21	10	11	0.91:1
3	No. 215	460	39	35	4	8.75:1
Total.....		20,242	3,158	2,384	774	3.08:1

TABLE 2 (continued)

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE- LEAVED	RATIO
1	No. 15	179	25	25	0	
1	No. 17	437	58	58	0	
1	No. 35	441	91	91	0	
1	No. 36	493	42	42	0	
1	No. 39	379	61	61	0	
1	No. 49	370	120	120	0	
1	No. 64	371	166	166	0	
1	No. 125	401	112	112	0	
1	No. 160a	436	47	47	0	
1	No. 164a	495	116	116	0	
1	No. 166	582	60	60	0	
1	No. 176	1,341	191	191	0	
2	No. 4	220	130	130	0	
2	No. 5	393	112	112	0	
2	No. 6	243	30	30	0	
2	No. 17	250	51	51	0	
2	No. 19	229	89	89	0	
2	No. 54	534	219	219	0	
2	No. 67	595	124	124	0	
3	No. 75	554	239	239	0	
3	No. 107	306	34	34	0	
3	No. 169	416	48	48	0	
Total.....		9,665	2,165	2,165	0	

This table shows the presence of homozygous and heterozygous dominants in the F_2 generation. The ratio of non-segregating to segregating cultures in this table is 22:41, which closely approximates the expected ratio, 1:2, of homozygous to heterozygous dominants in the F_2 generation.

TABLE 3

Analysis of the F_4 generation resulting from self-pollination of *f. typica* plants chosen at random from the non-segregating F_3 progenies (see table 2) of the cross *mut. formosa* $\times$ *mut. latifolia* C.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
1	No. 39-14	ca. 1,300† ⁶	254	254	0	
1	No. 39-24	ca. 1,100†	167	167	0	
1	No. 64-9	ca. 1,000†	109	109	0	
1	No. 125-44	ca. 750†	18	18	0	
1	No. 125-46	ca. 900†	85	85	0	
1	No. 125-48	ca. 800†	14	14	0	
1	No. 125-49	ca. 850†	26	26	0	
1	No. 166-9	ca. 1,200†	10	10	0	
1	No. 176-1	ca. 700†	20	20	0	
1	No. 176-13	ca. 900†	51	51	0	
2	No. 4-2	ca. 900†	47	47	0	
2	No. 4-3	ca. 800†	78	78	0	
2	No. 4-6	ca. 700†	15	15	0	
2	No. 4-16	ca. 1,200†	138	138	0	
2	No. 4-21	ca. 700†	69	69	0	
2	No. 54-6	ca. 600†	13	13	0	
Total.....		ca. 14,400	1,114	1,114	0	

All of the plants are flat-leaved, demonstrating further the presence of homozygous dominants in the F_2 generation of the cross. Of the 326 plants grown to maturity, taken in part from each of twelve cultures, 320 proved to be *f. typica* and of the remaining 6 plants 2 were *mut. nummularia*,⁷ 2 were *mut. fallax*, an undescribed mutation, as a seedling very much like *mut. nummularia* and thrown by the same strains, 1 was probably *mut. gigas*,⁸ and 1 resembled *mut. angustifolia*.⁹

TABLE 4

Analysis of the F_4 generation resulting from self-pollination of *f. typica* plants chosen at random from the segregating F_3 progenies (see table 2) of the cross *mut. formosa* $\times$ *mut. latifolia* C.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
1	No. 167b-12	ca. 550†	15	10	5	2.00:1
1	No. 167b-25	ca. 900†	165	132	33	4.00:1
Total.....		ca. 1,450†	180	142	38	3.74:1
1	No. 168-44	ca. 700†	25	25	0	

Of the three cultures, two are segregating and one is not, showing the presence of homozygous and heterozygous dominants in the F_3 generation from heterozygous F_2 plants. Of the 64 plants grown to maturity from the two segregating cultures 52 proved to be *f. typica*, 1 was *mut. fallax*, 10 were *mut. formosa*, and 1 was *mut. setacea*,¹⁰ which is a revolute-leaved type thrown by *mut. formosa*. All of the 25 plants of the non-segregating culture proved to be *f. typica*.

⁶ In this and subsequent tables the dagger (†) indicates that seeds from two or more capsules were sown together.

⁷ *Mut. nummularia*, a mutation commonly thrown by strain C, but never by pure strain E See BARTLETT 1915 a, p. 97; COBB and BARTLETT 1919.

⁸ See BARTLETT, 1915 b, p. 443.

⁹ See BARTLETT, 1915 b, p. 438.

¹⁰ See BARTLETT, 1915 b, p. 450.

TABLE 5

Analysis of the F_1 generation of the cross *mut. formosa* $\times$ *f. typica* C ($\alpha'\beta\beta \times \alpha\beta\beta$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
4		ca. 300†	7	7	0	
5		316†	10	10	0	
6		51* ¹¹	8	8	0	
7		327†	28	28	0	
8		57†	30	30	0	
9		33*	17	17	0	
Total.....		1,084	100	100	0	

The cultures consist of flat-leaved types only, but as seedlings the plants show the effect of crossing in irregularities in their leaves, the blades being unsymmetrically developed. Of the 95 plants grown to maturity, taken in part from each of the six cultures, all proved to be *f. typica* except 1 plant, which was an undescribed flat-leaved mutation, *mut. dimorpha*.

TABLE 6

Analysis of the F_2 generation resulting from self-pollination of *f. typica* plants chosen at random from the F_1 generation (see table 5) of the cross *mut. formosa* $\times$ *f. typica* C ($\alpha'\beta\beta \times \alpha\beta\beta$). Each of the cultures contains both flat-leaved and revolute-leaved plants in approximately a 3:1 ratio.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
4	No. 3	ca. 500†	165	132	33	4.00:1
4	No. 5	ca. 850†	67	54	13	4.15:1
4	No. 6	ca. 900†	452	337	115	2.93:1
5	No. 7	ca. 700†	87	69	18	3.83:1
5	No. 9	ca. 800†	346	243	103	2.36:1
6	No. 1	ca. 600†	208	155	53	2.92:1
6	No. 3	ca. 800†	121	86	35	2.46:1
6	No. 6	ca. 1,000†	111	81	30	2.70:1
6	No. 7	ca. 1,000†	483	347	136	2.55:1
6	No. 8	ca. 900†	244	181	63	2.87:1
7	No. 4	ca. 800†	286	220	66	3.33:1
7	No. 6	ca. 900†	202	141	61	2.31:1
7	No. 9	ca. 900†	182	120	62	1.94:1
7	No. 10	ca. 900†	200	146	54	2.70:1
8	No. 10	ca. 950†	120	87	33	2.64:1
Total.....		ca. 12,500	3,274	2,399	875	2.74:1

¹¹ The asterisk (*) in this and subsequent tables indicates that seeds from a single capsule were sown.

TABLE 7

Analysis of the F₁ generation of the cross f. typica C × mut. formosa (αβFF × α'βff).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
10		100†	63	63	0	
11		221*	50	50	0	
12		140*	88	88	0	
13		*	45	45	0	
14		186*	125	125	0	
15		†	176	176	0	
16		300†	235	235	0	
Total.....		947+	782	782	0	

The cultures consist of flat-leaved types only. Of the 389 plants grown to maturity, taken in part from each of the seven cultures, 381 were *f. typica*, and the remaining 8 were of other flat-leaved types—3 of *mut. fallax*, 2 of *mut. dimorpha*, 1 of *mut. grisella* (an undescribed mutation), and 2 undetermined mutations.

TABLE 8

Analysis of the F₂ generation resulting from self-pollination of f. typica plants chosen at random from the F₁ generation (see table 7) of the cross f. typica C × mut. formosa (αβFF × α'βff).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
10	No. 1	1,296†	545	533	12	
10	No. 2	1,425†	92	92	0	
10	No. 17	810†	174	174	0	
10	No. 25	681†	18	17	1	
10	No. 42	1,113†	142	142	0	
11	No. 32	1,265†	41	41	0	
11	No. 35	1,243†	17	16	1	
11	No. 37	1,428†	29	26	3	
11	No. 44	1,812†	8	7	1	
11	No. 50	1,574†	57	54	3	
12	No. 12	1,455†	3	2	1	
12	No. 14	1,693†	127	126	1	
12	No. 29	1,594†	5	4	1	
12	No. 36	1,214†	87	86	1	
12	No. 44	1,232†	309	308	1	
Total.....		19,835	1,654	1,628	26	61.5:1

The cultures consist of flat-leaved plants with a small percentage of revolute-leaved plants, considered to have arisen by separate mutations of the α gamete in the presence of the recessive allelomorphs of the Mendelian factors for flatness.

TABLE 9

Analysis of the F₁ generation of the cross mut. formosa × f. typica E (α'βff × αβff).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
17		258†	21	0	21	
18		471†	10	0	10	
19		535†	86	0	86	
20		157*	10	0	10	
21		150*	13	0	13	
22		167*	33	0	33	
23		100*	21	0	21	
24		138*	25	0	25	
25		866†	86	0	86	
Total.....		2,842	305	0	305	

All of the plants are revolute-leaved. Of the 235 plants grown to maturity, taken in part from each of the nine cultures, 230 were *mut. formosa*, and the remaining 5 were plants of other revolute-leaved types—3 of *mut. revoluta*,¹² 1 of *mut. selacea*, and 1 of *mut. albicans* (?),¹³ all of these being types thrown by pure strains of *mut. formosa*.

TABLE 10

Analysis of the F₂ generation resulting from self-pollination of f. typica plants chosen at random from the F₁ generation (see table 9) of the cross mut. formosa × f. typica E (α'βff × αβff).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
22	No. 24	ca. 800†	260	0	260	
23	No. 2	ca. 600†	111	0	111	
25	No. 63	ca. 800†	216	0	216	
18	No. 8	ca. 750†	41	0	41	
Total.....		ca. 2,950	628	0	628	

All of the plants are revolute-leaved, as in the F₁ generation of this cross; that is, the inheritance is matroclinic. Of the 72 plants grown to maturity, taken in part from each of the four cultures, all proved to be *mut. formosa*.

¹² See BARTLETT, 1915 b, p. 450.¹³ See BARTLETT, 1915 b, p. 449.

TABLE 11

Analysis of the F_1 generation of the cross *mut. formosa* $\times$ *f. typica* *M* (homozygous) ($\alpha'\beta ff \times \alpha'\beta FF$). The staminate parent belonged to the F_3 generation of the cross *mut. formosa* $\times$ *mut. latifolia* *C*.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
26		153†	113	113	0	
27		225†	69	69	0	
28		56*	12	12	0	
29		79*	30	30	0	
30		152†	26	26	0	
31		167†	42	42	0	
Total.....		832	292	292	0	

Each culture contains only flat-leaved plants. Of the 181 plants grown to maturity, taken in part from each of the six cultures, 160 proved to be *f. typica*, and the remaining 21 were of other flat-leaved types—16 were *mut. dimorpha*, 1 was *mut. fallax*, 1 was *mut. grisea* (an undescribed mutation), and 3 were undetermined.

TABLE 12

Analysis of the F_2 generation resulting from self-pollination of *f. typica* plants chosen at random from the F_1 generation (see table 11) of the cross *mut. formosa* $\times$ *f. typica* *M* (homozygous) ($\alpha'\beta ff \times \alpha'\beta FF$). Each of the cultures contains flat-leaved and revolute-leaved plants in approximately a 3:1 ratio.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
26	No. 41	ca. 1,400†	95	71	24	2.96:1
26	No. 3	ca. 2,000†	245	166	79	2.10:1
26	No. 9	ca. 1,200†	62	46	16	2.87:1
26	No. 25	ca. 1,200†	34	23	11	2.09:1
26	No. 46	ca. 2,100†	61	39	22	1.77:1
27	No. 3	ca. 2,200†	31	22	9	2.44:1
27	No. 15	ca. 2,050†	23	20	3	6.67:1
27	No. 16	ca. 2,050†	51	32	19	1.68:1
27	No. 20	ca. 2,100†	28	21	7	3.00:1
29	No. 6	ca. 1,500†	73	54	19	2.84:1
29	No. 12	ca. 1,150†	25	20	5	4.00:1
29	No. 16	ca. 1,100†	282	216	66	3.27:1
29	No. 18	ca. 1,650†	112	84	28	3.00:1
29	No. 25	ca. 1,650†	120	68	52	1.31:1
31	No. 4	ca. 1,800†	126	92	34	2.71:1
31	No. 6	ca. 1,900†	86	56	30	1.87:1
63	No. 1	ca. 8,900†	993	742	251	2.96:1
63	No. 2	ca. 4,600†	849	655	194	3.38:1
63	No. 3	ca. 1,450†	563	423	140	3.02:1
63	No. 4	ca. 1,500†	77	59	18	3.28:1
64	No. 13	ca. 2,300†	81	62	19	3.26:1
64	No. 15	ca. 2,500†	229	158	71	2.23:1
64	No. 17	ca. 2,100†	73	46	27	1.70:1
64	No. 23	ca. 2,000†	300	212	88	2.41:1
64	No. 24	ca. 2,300†	718	508	210	2.42:1
Total.....		ca. 54,700	5,337	3,895	1,442	2.70:1

TABLE 13

Analysis of the F_1 generation of the cross *f. typica* *M* (homozygous) $\times$ *mut. formosa* ($\alpha'\beta FF \times \alpha'\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
32		ca. 300†	48	48	0	
33		293†	122	122	0	
34		202†	18	18	0	
35		220†	27	27	0	
36		50*	33	33	0	
37		66†	45	45	0	
38		204†	122	122	0	
39		182†	23	23	0	
40		71†	36	36	0	
Total.....		ca. 1,588	474	474	0	

The pistillate parent belonged to the F_2 generation of the cross *mut. formosa* $\times$ *mut. latifolia* C. Each of the cultures consists of only flat-leaved plants. Of the 210 plants grown to maturity, taken in part from each of the nine cultures, 204 proved to be *f. typica*, and the remaining 6 were of other flat-leaved types,—3 were *mut. dimorpha*, 1 was *mut. fallax*, 1 was *mut. sub-latifolia* (?),¹⁴ and 1 was undetermined.

TABLE 14

Analysis of the F_2 generation resulting from self-pollination of *f. typica* plants chosen at random from the F_1 generation (see table 13) of the cross *f. typica* *M* (homozygous) $\times$ *mut. formosa* ($\alpha'\beta FF \times \alpha'\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
32	No. 3	ca. 1,750†	64	46	18	2.56:1
32	No. 4	ca. 1,700†	203	155	48	3.23:1
34	No. 7	ca. 1,900†	122	92	30	3.07:1
34	No. 9	ca. 1,650†	78	63	15	4.20:1
34	No. 13	ca. 1,950†	739	549	190	2.89:1
35	No. 4	ca. 1,600†	111	72	39	1.85:1
35	No. 7	ca. 1,275†	556	406	150	2.71:1
35	No. 11	ca. 1,600†	34	23	11	2.09:1
37	No. 11	ca. 2,150†	147	109	38	2.87:1
37	No. 16	1,353†	38	31	7	4.43:1
37	No. 21	ca. 1,850†	159	120	39	3.08:1
37	No. 23	1,103†	54	40	14	2.86:1
38	No. 5	ca. 1,900†	110	78	32	2.44:1
38	No. 6	ca. 1,900†	380	283	97	2.92:1
38	No. 24	ca. 2,600†	443	312	131	2.38:1
65	No. 1	ca. 1,400†	210	143	67	2.13:1
65	No. 4	ca. 1,450†	159	109	50	2.18:1
66	No. 1	ca. 700†	225	150	75	2.00:1
66	No. 2	ca. 700†	34	26	8	3.25:1
66	No. 3	ca. 1,600†	434	313	121	2.59:1
Total.....		ca. 32,131	4,300	3,120	1,180	2.64:1

Each of the cultures contains both flat-leaved and revolute-leaved plants, in approximately a 3:1 ratio. Of the 74 plants from three of these cultures, grown to maturity, 58 proved to be *f. typica* and 16 proved to be *mut. formosa*.

¹⁴ An undescribed mutation.

TABLE 15

Analysis of the F_1 generation of the cross *mut. formosa* $\times$ *f. typica* M (heterozygous) ($\alpha'\beta ff \times \alpha'\beta Ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
41		333†	13	5	8	0.63:1
42		64*	27	15	12	1.25:1
43		40*	19	7	12	0.58:1
Total.....		437	59	27	32	0.84:1

In the case of 41, the staminate parent belonged to the F_2 generation of the cross *mut. formosa* $\times$ *mut. latifolia* C; in the case of 42 and 43 to the F_2 generation of the cross *mut. formosa* $\times$ *hyb. viscida*.¹⁵ In each of the cultures flat-leaved and revolute-leaved plants occur, in about equal numbers. The expected ratio is 1:1. When the germination is poor, the number of revolute-leaved plants often slightly exceeds the expectation, as it does here. Of the 42 plants grown to maturity, taken in part from each of the three cultures, 21 were *f. typica* (one of them a dwarf), 3 were of other flat-leaved types (2 of *mut. graminea*,¹⁶ and 1 an undetermined mutation), 16 were *mut. formosa* (6 of them very poor plants) and 2 were *mut. revoluta*, which is one of the revolute-leaved mutations thrown by *mut. formosa*.

TABLE 16

Analysis of an F_2 progeny resulting from self-pollination of an *f. typica* plant of the F_1 generation (see table 15) of the cross *mut. formosa* $\times$ *f. typica* M (heterozygous) ($\alpha'\beta ff \times \alpha'\beta Ff$). The numbers of flat-leaved and revolute-leaved plants closely approximate a 3:1 ratio.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
41	No. 10	ca. 4,250†	1,849	1,348	501	2.69:1

TABLE 17

Analysis of the F_1 generation of the cross *f. typica* M (heterozygous) $\times$ *mut. formosa* ($\alpha'\beta Ff \times \alpha'\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
44		657†	117	58	59	1.98:1
45		319†	50	20	30	0.67:1
Total.....		976	167	78	89	0.88:1

The pistillate parent belonged to the F_2 generation of the cross *mut. formosa* $\times$ *mut. latifolia* C. In these cultures flat-leaved and revolute-leaved plants occur in about equal numbers, but, as in the reciprocal cross, the number of revolute-leaved plants slightly exceeds that required for the expected 1:1 ratio. Of the 88 plants grown to maturity, taken in part from each of the two cultures, 36 were *f. typica*, 2 were of other flat-leaved types (1 of *mut. ericacea*¹⁷ and 1 dwarf), and 50 were *mut. formosa*, one of them bearing a flat-leaved bud-sport.

¹⁵ *Hyb. viscida*, a hybrid of *Oenothera pratincola* $\times$ *Oe. numismatica* (see BARTLETT 1915 a, p. 86). This form is like *Oe. pratincola* *f. typica* with the addition of the viscid pubescence of *Oe. numismatica*.

¹⁶ Regarding *mut. graminea*, see BARTLETT 1915 b, p. 429.

¹⁷ An undescribed mutation.

TABLE 18

Analysis of the F_2 generation resulting from self-pollination of *f. typica* plants chosen at random from the F_1 generation (see table 17) of the cross *f. typica M* (heterozygous) $\times$ *mut. formosa* ($\alpha'\beta Ff \times \alpha'\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
45	No. 12	ca. 750†	157	114	43	2.65:1
46	No. 2	ca. 600†	22	16	6	2.66:1
44	No. 14	ca. 900†	18	14	4	3.50:1
44	No. 17	ca. 800†	463	344	119	2.89:1
Total.....		ca. 3,050	660	488	172	2.84:1

Each of the cultures contains both flat-leaved and revolute-leaved plants, in approximately a 3:1 ratio. Of the 50 plants from one culture grown to maturity, 42 proved to be *f. typica* and 8 proved to be *mut. formosa*.

TABLE 19

Analysis of an F_1 progeny of the cross *f. typica E* $\times$ *f. typica M* (homozygous) ($\alpha\beta ff \times \alpha'\beta FF$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
47		95†	78	78	0	

The staminate parent belonged to the F_2 generation of the cross *mut. formosa* $\times$ *mut. latifolia* C. All of the plants are flat-leaved. Of the 49 plants grown to maturity, 44 were *f. typica*, and the remaining 5 were of other flat-leaved types—2 of *mut. ericacea*, 2 of *mut. dimorpha*, and 1 undetermined mutation.

TABLE 20

Analysis of the F_2 generation resulting from self-pollination of *f. typica* plants chosen at random from the F_1 generation (see table 19) of the cross *f. typica E* $\times$ *f. typica M* (homozygous) ($\alpha\beta ff \times \alpha'\beta FF$). In each culture all of the plants are flat-leaved.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
47	No. 4	ca. 1,700†	1,016	1,016	0	
47	No. 8	ca. 1,800†	1,265	1,265	0	
47	No. 11	ca. 1,000†	813	813	0	
47	No. 15	1,205†	91	91	0	
47	No. 19	ca. 1,400†	1,140	1,140	0	
47	No. 26	1,436†	1,062	1,062	0	
47	No. 28	ca. 1,500†	533	533	0	
47	No. 30	1,214†	169	169	0	
Total.....		ca. 11,255	6,089	6,089	0	

TABLE 21

Analysis of the F_1 generation of the cross *f. typica M* (homozygous) $\times$ *f. typica E* ($\alpha'\beta FF \times \alpha\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
48		194†	21	21	0	
49		392†	238	238	0	
50		197†	128	128	0	
51		361†	275	275	0	
52		50†	32	32	0	
Total.....		1,194	694	694	0	

The pistillate parent belonged to the F_2 generation of the cross mut. *formosa* $\times$ mut. *latifolia* C. Each of the cultures contains only flat-leaved plants. Of the 157 plants grown to maturity, taken in part from each of the five cultures, 155 proved to be *f. typica*, and the remaining 2 were mut. *fallax*.

TABLE 22

Analysis of the F_2 generation resulting from self-pollination of *f. typica* plants chosen at random from the F_1 generation (see table 21) of the cross *f. typica M* (homozygous) $\times$ *f. typica E* ($\alpha'\beta FF \times \alpha\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
50	No. 40	1,425†	629	465	164	2.84:1
50	No. 44	1,529†	461	337	124	2.72:1
51	No. 12	1,345†	612	445	167	2.66:1
53	No. 1	ca. 1,000†	494	367	127	2.88:1
53	No. 2	ca. 900†	31	23	8	2.88:1
53	No. 3	ca. 1,000†	17	12	5	2.40:1
53	No. 4	ca. 750†	10	7	3	2.33:1
53	No. 5	ca. 400†	33	22	11	2.00:1
53	No. 6	ca. 900†	12	11	1	11.00:1
Total.....		ca. 9,249	2,299	1,689	610	2.77:1

Each of the cultures contains flat-leaved and revolute-leaved plants, in approximately a 3:1 ratio. Of the 25 plants from one culture grown to maturity, 22 proved to be *f. typica*, 1 was of another flat-leaved type (mut. *démorpha*), and 2 were mut. *formosa*.

TABLE 23

Analysis of the F_1 generation of the cross *f. typica* M (heterozygous) $\times$ *f. typica* E ($\alpha'\beta Ff \times \alpha\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
54		528†	42	20	22	0.91:1
55		401†	12	6	6	1.00:1
56		430†	86	34	52	0.65:1
57		301†	34	22	12	1.83:1
Total.....		1,660	174	82	92	0.89:1

The pistillate parent belonged to the F_2 generation of the cross mut. *formosa* $\times$ mut. *latifolia* C. In each of the cultures flat-leaved and revolute-leaved plants occur in about equal numbers. The expected ratio is 1:1. When the germination is poor, the number of revolute-leaved plants often slightly exceeds the expectation, as it does here. Of the 112 plants grown to maturity, taken in part from each of the four cultures, 56 were *f. typica*, 4 were of other flat-leaved types (1 was mut. *fallax* and 3 were of a dwarf type), 51 were mut. *formosa*, and 1 was mut. *revoluta*, which is one of the revolute-leaved mutations thrown by mut. *formosa*.

TABLE 24

Analysis of the F_2 generation resulting from self-pollination of *f. typica* plants chosen at random from the F_1 generation (see table 23) of the cross *f. typica* M (heterozygous) $\times$ *f. typica* E ($\alpha'\beta Ff \times \alpha\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
54	No. 3	ca. 900†	198	153	45	3.40:1
57	No. 20	ca. 1,000†	228	167	61	2.74:1
57	No. 22	ca. 1,000†	55	41	14	2.93:1
57	No. 24	ca. 800†	12	10	2	5.00:1
57	No. 25	ca. 500†	101	79	22	3.59:1
57	No. 28	ca. 750†	107	86	21	4.10:1
Total.....		ca. 4,950	701	536	165	3.25:1

Each of the cultures contains both flat-leaved and revolute-leaved plants in approximately a 3:1 ratio. Of the 49 plants from one culture grown to maturity, 34 proved to be *f. typica* and 15 proved to be mut. *formosa*.

TABLE 25

Analysis of the F₁ generation of the cross f. typica M (homozygous) × f. typica C (α'βFF × αβFF).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
58		82*	57	57	0	
59		109†	11	11	0	
Total.....		191	68	68	0	

The pistillate parent belonged to the F₂ generation (in the case of 59) and the F₃ generation (in the case of 58) of the cross mut. *formosa* × mut. *latifolia* C. All of the plants are flat-leaved, and when grown to maturity all proved to be f. *typica*.

TABLE 26

Analysis of the F₂ generation resulting from self-pollination of f. typica plants chosen at random from the F₁ generation (see table 25) of the cross f. typica M (homozygous) × f. typica C (α'βFF × αβFF). All of the plants are flat-leaved.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
59	No. 3	ca. 400†	3	3	0	
59	No. 7	ca. 600†	2	2	0	
58	No. 1	1,664†	9	9	0	
58	No. 2	1,500†	20	20	0	
58	No. 5	1,647†	280	280	0	
58	No. 12	1,423†	230	230	0	
Total.....		ca. 7,234	544	544	0	

TABLE 27

Analysis of the F₁ generation of the cross f. typica M (heterozygous) × f. typica C (α'βFf × αβFF).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
60		225†	9	9	0	
61		247†	7	7	0	
62		318+†	50	50	0	
Total.....		790+	66	68	0	

The pistillate parent belonged to the F₂ generation of the cross mut. *formosa* × mut. *latifolia* C. Each of the cultures contains only flat-leaved plants. Of the 66 plants grown to maturity, taken in part from each of the three cultures, 65 proved to be f. *typica*, and the remaining 1 was mut. *fallax*.

TABLE 28

Analysis of the F₂ generation resulting from self-pollination of f. typica plants chosen at random from the F₁ generation (see table 27) of the cross f. typica M (heterozygous) × f. typica C (αβFf × αβFF).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
60	No. 1	ca. 1,200†	839	839	0	
60	No. 4	ca. 1,300†	887	887	0	
60	No. 5	ca. 700†	239	239	0	
60	No. 6	ca. 900†	487	487	0	
60	No. 9	ca. 1,700†	1,066	1,066	0	
61	No. 2	675†	399	399	0	
61	No. 3	ca. 1,100†	465	465	0	
62	No. 8	ca. 550†	109	109	0	
62	No. 9	ca. 800†	80	80	0	
62	No. 19	ca. 400†	52	52	0	
62	No. 33	ca. 700†	48	48	0	
Total.....		ca. 10,025	4,671	4,671	0	
60	No. 3	1,011†	286	213	73	2.92:1
60	No. 8	ca. 1,200†	378	308	70	4.40:1
61	No. 1	773†	109	88	21	4.19:1
61	No. 6	ca. 1,300†	892	698	194	3.60:1
62	No. 36	ca. 600†	20	17	3	5.67:1
61	No. 4	ca. 1,000†	561	470	91	5.16:1
61	No. 5	ca. 1,500†	1,128	830	298	2.79:1
Total.....		ca. 7,384	3,374	2,624	750	3.50:1

Of the eighteen progenies, eleven consist entirely of flat-leaved plants and seven consist of flat-leaved and revolute-leaved plants in approximately a 3:1 ratio. The ratio 11:7 does not approach as closely as expected, to the 1:1 ratio of gametes bearing the dominant factor to gametes bearing the recessive factor, produced by the heterozygous pistillate parent of the cross.

TABLE 29
A summary of tables 5 to 28 inclusive.

PARENTS		F ₁ GENERATION						F ₂ GENERATION			
	Constitution	Table number	Type of plants	Constitution	Total plants	Ratio flat to revolute	Table number	Type of plants	Constitution	Total plants	Ratio flat to revolute
mut. <i>formosa</i> × <i>f. typica</i> C	α'βff × αβFFF	5	flat	α'βFf	100		6	flat	{α'βFFF α'βFf	3,274	2.75:1
	αβFFF							revolute	α'βff		
<i>f. typica</i> C × mut. <i>formosa</i>	αβFFF × α'βff	7	flat	αβFf	782		8	flat	{αβFFF αβFf αβff	1,628	26
	α'βff							revolute mut.	α'βff		
mut. <i>formosa</i> × <i>f. typica</i> E	α'βff × αβff	9	revolute	α'βff	305		10	revolute	α'βff	628	
	αβff							flat	αβff		
<i>f. typica</i> E × mut. <i>formosa</i>	αβff × α'βff	(See COBB and BART-LETT 1919, table 1)	flat revolute mut.	α'βff	11 122		(See COBB and BART-LETT 1919, table 1)	flat	αβff	103	
	α'βff							revolute mut.	α'βff		
mut. <i>formosa</i> × <i>f. typica</i> M (homozygous)	α'βff × α'βFFF	11	flat	α'βFf	292		12	flat	{α'βFFF α'βFf	5,337	2.70:1
	α'βFFF							revolute	α'βff		
<i>f. typica</i> M (homozygous) × mut. <i>formosa</i>	α'βFFF × α'βff	13	flat	α'βFf	474		14	flat	{α'βFFF α'βFf	4,300	2.65:1
	α'βff							revolute	α'βff		

mut. <i>formosa</i> × f. <i>typica</i> M (heterozygous)	$\alpha'\beta ff$ × $\alpha'\beta Ff$	15	flat	$\alpha'\beta Ff$	59	0.85:1	16	flat	$\left\{ \begin{matrix} \alpha'\beta FF \\ \alpha'\beta Ff \end{matrix} \right.$	1,849	2.69:1
f. <i>typica</i> M (heterozygous) × mut. <i>formosa</i>	$\alpha'\beta Ff$ × $\alpha'\beta ff$	17	flat	$\alpha'\beta Ff$	167	0.88:1	18	flat	$\left\{ \begin{matrix} \alpha'\beta FF \\ \alpha'\beta Ff \end{matrix} \right.$	660	2.83:1
f. <i>typica</i> E × f. <i>typica</i> M (homozygous)	$\alpha\beta ff$ × $\alpha'\beta FF$	19	flat	$\alpha\beta Ff$	78		20	flat	$\left\{ \begin{matrix} \alpha\beta FF \\ \alpha\beta Ff \\ \alpha\beta ff \end{matrix} \right.$	6,089	2.77:1
f. <i>typica</i> M (homozygous) × f. <i>typica</i> E	$\alpha'\beta FF$ × $\alpha\beta ff$	21	flat	$\alpha'\beta Ff$	694		22	flat	$\left\{ \begin{matrix} \alpha'\beta FF \\ \alpha'\beta Ff \end{matrix} \right.$	2,299	
f. <i>typica</i> M (heterozygous) × f. <i>typica</i> E	$\alpha'\beta Ff$ × $\alpha\beta ff$	23	flat	$\alpha'\beta Ff$	174	0.89:1	24	flat	$\left\{ \begin{matrix} \alpha'\beta FF \\ \alpha'\beta Ff \end{matrix} \right.$	701	3.24:1
f. <i>typica</i> M (homozygous) × f. <i>typica</i> C	$\alpha'\beta FF$ × $\alpha\beta FF$	25	flat	$\alpha'\beta FF$	68		26	flat	$\alpha'\beta FF$	544	
f. <i>typica</i> M (heterozygous) × f. <i>typica</i> C	$\alpha'\beta Ff$ × $\alpha\beta FF$	27	flat	$\alpha'\beta Ff$	66		28	flat	$\left\{ \begin{matrix} \alpha'\beta FF \\ \alpha'\beta Ff \end{matrix} \right.$	4,671	
								revolute	$\alpha'\beta ff$	3,374	3.50:1

TABLE 30

Ratios of flat-leaved to revolute-leaved plants (given in terms of flat-leaved plants per thousand germinations) in all cultures in which the expectation is 750, assembled and classified according to percentage of germination.

Number of flat-leaved plants per thousand plants in each of the cultures of the accompanying tables in which the expected number is 750	PERCENTAGE OF GERMINATION										
	1-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-81
627	476	611	681	635	652	667	708	702	718	736	
630	567	655	682	658	677	731	743	713	727	746	
639	606	678	704	678	720	745	751	729	742	772	
651	649	685	707	697	742	750	769	730		780	
652	667	712	711	717	745	799	808	739		838	
667	690	725	737	726	786	815	812				
676	709	730	748	730	800						
676	730	743	750	732							
700	739	747	771	737							
706	742	754	800	744							
710	742	763		744							
719	743	789		756							
727	745	789		762							
739	747	793		772							
741	750	795		782							
742	750	804		830							
750	755	808		854							
765	766	825		914							
765	806	836									
766	815										
778	818										
800	897										
808	917										
816											
833											
850											
863											
869											
917											
Average...	744	732	750	729	748	732	751	765	726	729	774