THE GENETIC BEHAVIOUR OF THE HYBRID *PRIMULA KEWENSIS*, AND ITS ALLIES.

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Introduction.

The first *Primula Kewensis* was found growing among plants of *P. floribunda*, and was thought to be an accidental hybrid of *floribunda* × *verticillata*. After a period of sterility it gave rise to a perfectly fertile form of larger size widely known as a greenhouse plant, and it is to this form that the name *P. Kewensis* is generally applied.

Inasmuch as the fertile *Kewensis*, though of hybrid origin, breeds in general true, throwing at all events no plants like *floribunda* or *verticillata*, a definite problem is thus created, and our object was to investigate this case of absence of segregation.

The fertile *Kewensis* was moreover shown by Miss Digby to be a tetraploid form having double the number of chromosomes possessed by *verticillata* or *floribunda* or the original hybrid, and we hoped also to investigate the genetics of this condition. This part of the investigation remains however incomplete, and will be the subject of a later paper.

Our experiments have consisted in breeding the various forms on a considerable scale, and in making all possible cross-fertilizations between them. As regards the results of self-fertilization, in our experience the species breed true except that *floribunda* throws a definite pale-flowered recessive, called *isabellina*. The tetraploid *Kewensis* breeds true approximately, the only evident segregation being in regard to mealiness of the foliar parts. This is a recessive condition but it appears in numerous intergrading states, the interrelations of which have not been successfully analysed.

We find the consequence of crossing between any two of the forms is that almost always the resulting offspring exactly *reproduce the maternal form, showing no paternal influence.*

In such a case the obvious suggestion is that we have to deal either with actual parthenogenesis or with the phenomenon denoted by the term monolepsis, a condition, that is to say, in which the ovules need the stimulus of fertilization for their development, though they take no genetic contribution from the pollen grains. Under most stringent tests positive evidence of true parthenogenesis has been obtained; but in view of all the facts we incline to suppose that the ovules are such that while they can occasionally develop without fertilization they more commonly develop in consequence of that stimulus.

The offspring of the tetraploid *Kewensis* both on selfing and crossing being simply a reproduction of the maternal type, no fresh recombinations can in general be made, but perhaps the most interesting part of our evidence relates to the production of a single diploid individual from *Kewensis* which, in striking contrast to the behaviour of the tetraploid, has exhibited segregation of an almost normal kind.

The plant in question was raised from the self-fertilization of a *Kewensis* which had been itself raised by fertilizing *Kewensis* with *floribunda*. Among its offspring are various new colours and combinations of characters unlike any that have appeared before in cultivation. Owing to intergradation it has not been found possible hitherto to make a quite satisfactory or complete factorial analysis of these types, though their genetic nature and properties are now fairly clear.

An interesting feature of these experiments lies in the fact that the parent species dealt with differ in respect of the floral dimorphism characteristic of the Primulaceæ. Whereas *floribunda* is heterostyle, *verticillata* is monomorphic, a condition only found in about five species of Primulaceæ.

The story of the origin of *P. Kewensis* is now well known to horticulturists. It appeared at Kew in 1900, among plants of *P. floribunda*, and was then thought to be a hybrid between *P. floribunda* and *P. verticillata*, and this was subsequently proved to be the case. According to the story often repeated in horticultural journals, the first hybrids obtained were sterile. The plant was described and figured in the *Gardeners' Chronicle*, 1900, pp. 130 and 195. From this drawing we presume that the anthers were in the thrum position, a feature of some interest in the light of the future history of the plant. The hybrid was propagated vegetatively and distributed by Messrs Veitch (Pl. XXV, fig. 3). No viable seed was obtained until about the year 1905, when a single plant bore seed. The following description of this plant is given in the *Gardeners' Chronicle*, Nov. 1911, p. 378: "This plant was, as we learn from Messrs Veitch, remarkable in several ways. In the first place its main inflorescence bore pin-eyed (long styled) flowers. In the second place, though the style of the flowers was long, the stamens were in the position which they occupy in thrum-eyed flowers. In other words the flowers, though pin-eyed as judging by their styles, were thrum-eyed as far as their stamens were concerned. In the third place other inflorescences which developed on this long styled plant bore ordinary thrum-eyed flowers. *Self-pollination* of the pin-eyed flowers resulted in the production of good seed, from which have been raised all the fertile plants of *P. Kewensis* now in cultivation."

We have little personal knowledge of this form. The tetraploid type is abundant in cultivation, and on its introduction the diploid gradually disappeared. Only recently have we been able, by the help of Mr Coutts, to obtain a specimen which will be the subject of further investigation.

We have been informed by Mr Garrett and Mr Coutts of the Royal Gardens, Kew, that the fertile *Kewensis* thus obtained differed in appearance from the sterile hybrid. We will refer to these differences later, but a more important difference was discovered by Miss Digby[1]. She found that whereas *P. verticillata*, *P. floribunda*, and the sterile hybrid have 18 chromosomes diploid number and 9 haploid number the fertile hybrid has 36 diploid and 18 haploid, being thus in the condition now called tetraploid. Moreover Digby and Farmer have since found that the chromosomes of the tetraploid are smaller than those of the diploid form[2].

Both at Kew and at Messrs Veitch's nursery, the cross between *verticillata* and *floribunda* was repeated; experience showed that the hybrid *Kewensis* is obtained very rarely, and that in the majority of cases the offspring are so-called "maternal hybrids,' *i.e.* they resemble the female parent.

Throughout this paper the term *Kewensis*, unless qualified, refers to the tetraploid form.

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[1] L. Digby, *Ann. Bot.* Vol. xxvi. No. 102, April, 1912.

[2] Farmer and Digby, *Phil. Trans. R. S.*, B. 205, p. 1.

STERILITY.

Before proceeding to a detailed description of our experiments, we must refer to the very important part played by sterility. In crossing the parent species with each other or with the hybrid *Kewensis*, viable seed has only rarely been obtained. In these crosses the ovary may fail altogether to swell, or the ovary may swell and very poor seed be obtained, some of which may germinate. On the other hand, we have often obtained apparently good seed, of which none, or only one or two seeds, have germinated. We have sometimes also got apparently good seed which has failed to germinate from *Kewensis* selfed. The method of culture has been to sow the seeds directly they are ripe, or a few weeks later. The results have been the same with both methods. There has been occasional difficulty in germinating seeds of *verticillata* and *floribunda*, but we regard these species as fully fertile, and in practice the fertility of *Kewensis* is not sensibly less. The condition of the diploid form is not accurately known.

HETEROSTYLY.

It is possible that some at least of the sterility observed is due to the fact that the parent species are respectively monomorphic and dimorphic as regards their flower structure. The two forms of flowers found in heterostyle species are usually referred to as "pin" or long styled and "thrum" or short styled respectively. The anthers in the pin form are at the base of the corolla tube: the style is long and may even protrude slightly beyond the corolla tube. In the thrum form the anthers are situated near the mouth of the corolla tube, while the style is very short and extends only a little way into the corolla tube.

In the monomorphic types such as *P. verticillata* the anthers are always near the mouth of the corolla tube, the style is long, but its length is variable, the stigma being sometimes on a level with the anthers, sometimes below the anthers, and sometimes above them.

P. floribunda exhibits heterostyly differing from the usual condition. The pin form is typical, but in the thrum form we have an arrangement resembling that found in *verticillata*. The anthers are always near the mouth of the corolla tube while the pistil is long styled. The stigma may be on a level with the anthers, or it may lie above them or below them, but we have not seen any plant with the style as short as in the normal thrum condition described above.

P. Kewensis resembles *P. verticillata* in being monomorphic.

POLLEN.

Darwin was the first to show that there was a structural difference between the pollen grains of the two types in dimorphic primulas, those of the "thrum" plants having a larger diameter than those of "pin" plants.

In *P. verticillata*, where only one form exists, we have not seen differences in size between pollens. The pollen of *Kewensis* is very irregular in size, and a large number of grains are bad. Scott[1] regards *P. verticillata* as being functionally dimorphic, because he found that on self-fertilization often no seed was obtained; but when fertilized by pollen from another plant the percentage of seed was greatly increased. We have no evidence on this point as we have only self-fertilized *verticillata*.

DESCRIPTION OF TYPES.

In 1911 we began a series of experiments in order to investigate and test the interesting results already obtained at Kew and elsewhere. By the kindness of the authorities at Kew, and Messrs Veitch, we were supplied with abundant material for the purpose.

P. floribunda. Pl. XXV, fig. 1. Whole plant covered with glandular jointed hairs; these are of two kinds, long many celled pointed hairs and short glandular hairs. Leaves 3—6 inches long, ovate, broadly toothed, petiole broad. Scapes numerous, 4—8 inches high, bearing superposed whorls of 3—6 flowers, subtended by an involucre of 3 or 4 bracts. Corolla golden yellow, limb flat, obcordate. Scentless. Heterostyled: in the long styled form the stigma is at the mouth of the corolla tube, and the stamens are near the base of the tube: the "thrum" form has a long style, with the stigma and the stamens at the mouth of the tube. There are slight variations in these relative positions. Pollen of "thrum" 5 μ, of "pins" 4 μ in diameter. Habitat Himalayas; figured *B.M.* t. 6172, vol. 39, 3rd series. Sir George Watt[2] gives a description of *P. floribunda* in its native habitat: "*P. flor.* occurs in clefts on damp rocks from Kumaon to Simla and Kashmir at altitudes from 3500—6000 ft. In its area however the altitude is gradually lowered on passing westward until in the N. Punjab it occurs almost at the level of the plains, and, what is perhaps more significant still, with

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[1] J. Scott, *Journ. Linn. Soc.* Vol. VIII. 1865.

[2] Sir George Watt, *J. R. H. S.*, "Report of Primula Conference," Aug. 1915, p. 196, reprinted from *J. R. H. S.*, 1904, p. 295.

the depression of altitude the plant becomes large, more robust, quite glabrous, often mealy, and the bracts foliaceous. General Sir J. M^cDonald sent me many years ago samples of the plant from the Khyber Pass. These in my opinion break down the separation of *P. verticillata* (the Abyssinian member of this series) from *P. floribunda*." A further statement differing slightly in detail is given in *J. R. H. S.*, Nov. 1914, p. 263.

P. floribunda var. *isabellina*. This variety was brought out by Haage and Schmidt in 1897, and was described by them as having pale sulphur coloured flowers. We have not been able to obtain any further information as to its origin. It is recessive to the full yellow form, and exists both in the thrum and pin form.

P. verticillata. Pl. XXV, fig. 2. Whole plant covered with meal. On the seedlings, before meal develops, short glandular hairs can be seen, as in *Kewensis*, and may be made visible in the full grown plant by dissolving the meal in alcohol. Leaves spathulate, 6—12 in. long, with long broad petioles, acutely toothed. Scapes 9 inches high and upwards, superposed whorls subtended by 4—6 leafy bracts. Flowers pale yellow. Corolla tube 1 inch long. Sweet scented. Homostyled: the anthers at the mouth of the corolla tube, the stigma at the same level or slightly protruding. Pollen 6·1 μ in diameter, uniform in size. Habitat Abyssinia. Figured in *B. M.*, t. 6042, vol. 29, 3rd series.

P. Kewensis. Sterile diploid hybrid. Pl. XXV, fig. 3. This hybrid was described in the *Gard. Chron.* Mar. 3, 1900, p. 130. From this description we have made the following abstract: Leaves 6—8 in. long, obovate-spathulate, with a long petiole-like base, the margins wavy and dentate, slightly mealy, otherwise glabrous. Scapes numerous, 12 inches long, with from 2—4 whorls of large leafy bracts, subtending whorls of from 6—10 flowers. Corolla tube 1 inch long, faintly mealy, bright yellow. Figured in *Gard. Chron.* March 1900, p. 195. It appears from this figure that the anthers were at the mouth of the tube.

P. Kewensis. Pl. XXVIII, figs. 9 and 10. Fertile tetraploid hybrid. As above but of more robust habit, leaves broader. In the F_1 hybrids the meal is confined to the calyx and corolla tube, but in succeeding generations there is great variation in the amount of meal. *P. Kewensis* v. *farinosa*, an interesting derivative variety, first raised by Messrs Veitch, is mealy all over. Short glandular hairs are present, as in *verticillata*. Sweet scented. The anthers are in the thrum position but the style varies in length. Pollen from 6·1—6·6 μ. We have examined a very large number of *Kewensis* plants of our own growing, and we have also been kindly allowed to examine stocks in various nurseries. We have never seen true heterostyly in *Kewensis*; although the styles may vary in length, the anthers are always in the thrum position. The pollens examined microscopically never show the difference in size which is so marked a feature in heterostyled primulas.

We have also examined a very large number of plants with regard to the condition of the leaf surface, and we find on careful inspection that many of the plants are really hairy. The hairs are short and sparsely scattered, sometimes visible to the naked eye, but often only to be seen with the aid of a lens.

We shall refer to this tetraploid form as *Kewensis*, and the sterile hybrid we shall refer to as diploid *Kewensis*.

EVIDENCE FROM CROSS-FERTILIZATION, AND THE QUESTION OF PARTHENOGENESIS.

We began our experiments in 1911 by crossing *verticillata* with *floribunda*, and in 1912 we also made many crosses between these species and *Kewensis*. We obtained offspring which resembled the maternal parent exactly, and which generally bred true on self-fertilization. These results were in accordance with those obtained in recent years at Kew and at Messrs Veitch's.

We then started a series of experiments in 1913 to find out if parthenogenesis actually occurs. The plants were carefully emasculated and isolated. In 1914 we repeated the experiments with additional precautions, isolating the plants in glass cages, which ensures isolation but has the disadvantage of bad ventilation. Nevertheless we obtained some positive evidence of parthenogenesis.

One of the difficulties we have had to contend with in this work has been the difference in the behaviour of the flowers of the same plant on crossing. Several flowers may be pollinated by the same male parent, one only may produce viable seed, the rest either giving seed which fails to germinate or none at all. On account of these irregularities, and of the uncertain germination of the seeds, it is impossible to lay much stress on the details; we shall therefore only consider the general course of the results.

There is some evidence that individual plants, though alike in their power of giving good seed when selfed, yet differ as regards the capacity for giving good seed on cross-fertilization. For instance, a single plant of *floribunda* var. *isabellina* was crossed with six *Kewensis* fathers, and in four of these crosses maternal hybrids were obtained; the two other crosses failed. Two of the maternal hybrids thus obtained were crossed again with *Kewensis*, and one of them gave maternal hybrids. On the other hand there is a case in which a *Kewensis* plant was fertilized by four *verticillata* fathers, one cross only gave offspring, the rest failed.

From 91 crosses of *verticillata* × *floribunda* and reciprocal, *Kewensis* appeared only twice. In each case one plant only was obtained and both these plants were fully fertile and bred true to *Kewensis*. The chromosomes of one hybrid were counted by Miss Digby, who found the haploid number to be 18 and the diploid number 36. We have never obtained the diploid original form of *Kewensis* as a result of our crosses. We may note here that *floribunda* and *verticillata* have never reappeared from the self-fertilization of *Kewensis*.

Of 28 plants of *verticillata* used as females in crosses with *floribunda* and *Kewensis*, 7 gave maternal hybrids. Of 17 plants of *verticillata* tested for parthenogenesis, one only gave viable seed. Of *floribunda*, 39 plants were used as females in crossing, 9 gave maternal hybrids. Ten plants of *floribunda* were tested for parthenogenesis, and gave no seed. Of *Kewensis*, 34 plants were used as females for crossing, and 11 gave maternal hybrids. Twelve plants of *Kewensis* were tested for parthenogenesis; 3 gave viable seed.

Tested by the viability of the seeds there is no great difference between the results of crossing and those obtained in the trials for parthenogenesis; but judged by their appearance there is a good deal of difference. In the crosses, the seed is often described as fair or good, whereas in the parthenogenesis tests only once from a *verticillata* did we obtain any seed described as good, and once seed described as fair from *Kewensis*.

Taking into consideration that the plants were in a glass cage, and the irregularities previously mentioned, the possibility that the "maternal hybrids" are parthenogenetic in origin cannot be said to be removed. The question must for the present be left open. We are continuing the experiments this year[1].

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[1] Perhaps in favour of the view that these offspring are parthenogenetic is the fact that using the pollen of *P. Forrestii*, a species far removed from this group, maternal offspring were obtained from *verticillata*.

EVIDENCE OF SEGREGATION IN *KEWENSIS*.

The types used, however fertilized, in general give nothing but plants resembling the seed parent. *P. floribunda, floribunda isabellina,* and *verticillata*, except in three isolated cases enumerated below, which we regard as errors, have given no offspring not identical with themselves. *P. Kewensis* moreover, though a hybrid, commonly throws nothing like the species from which it is derived. Among *Kewensis* families there may be some variation, notably in the size of the plants or in the amount of meal present, and in respect of this last character the evidence points to the occurrence of segregation. One example of variation in colour occurred, and a double form has also arisen.

We have further to record a group of seven cases in which solitary individuals of unexpected nature came from *Kewensis* seed. These may not impossibly be due to errors, but for certain reasons we are disposed to regard them as instances of segregation occurring sporadically.

But the most remarkable departure from the usual genetic behaviour of these plants was the appearance, on at least one occasion[1], of a diploid individual as the offspring of the tetraploid type, and on breeding from this individual we raised families in which segregation is habitual and probably runs a normal course.

These several statements may now be amplified.

A. Aberrant cases probably due to error.

(1) A family of *verticillata* plants was sent us from Kew, arising from *vert.* × *flor.* One of these plants on self-fertilization gave a large number of *verticillata* plants and one plant of *floribunda.*

(2) A plant of *floribunda* var. *isabellina* (extracted from a cross with a diploid plant which came from *Kewensis*, no. $\frac{18}{12}$) on self-fertilization gave 28 plants, one of which had *yellow* flowers, the rest with the pale flowers of *isabellina.* The plant with yellow flowers differed from the others in several respects. This is the only case we have met with of the *isabellina* type not breeding true.

(3) A plant of *floribunda*, long styled or pin (the recessive form), extracted from a cross with a diploid form which came from *Kewensis*, no. $\frac{18}{12}$, on selfing gave three *thrums* and four pins. This is the only case we have had of a pin plant not breeding true.

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[1] Only in one of these cases have the chromosomes been counted. In one other case, the *floribunda*-like habit of the plants in question suggest that they are diploid.

B. Aberrant cases possibly due to segregation in *Kewensis.*

In 1912, three plants of *Kewensis* were given us by the Botanic Gardens, Cambridge, and were numbered $\frac{22}{12}$, $\frac{28}{12}$ and $\frac{41}{12}$. They were used in the following crosses:—

(1) *vert.* × *Kewensis* $\frac{22}{12}$ *Kewensis* $\frac{28}{12}$ selfed
maternal hybrids of which a plant $\frac{7}{14}$ × *Kewensis* $\frac{178}{14}$ a plant
One plant only, *floribunda.*

(2) *flor.* × *vert.* 1911
maternal hybrids of which a plant $\frac{21}{12}$ × *Kewensis* $\frac{28}{12}$
maternal hybrids of which a plant $\frac{1}{13}$ × $\frac{28}{12}$ [reciprocal cross below]
1 plant only, *verticillata.*

(3) *Kewensis* $\frac{28}{12}$ × $\frac{1}{13}$
1 plant only, *verticillata.*
Compare reciprocal above.

(4) *floribunda* var. *is.* × 2*x Kewensis* (at Messrs Veitch)
maternal hybrids
Kewensis $\frac{41}{12}$ × $\frac{7}{12}$ a plant
1 plant only, *floribunda* yellow.

Two other aberrant cases unconnected with the above occurred.

(5) *Kewensis* × *flor.* var. *is.* (at Messrs Veitch)
maternal hybrids
flor. var. *is.* × $\frac{18}{12}$ a plant
2 plants only of which
1 = *floribunda* yellow,
1 = *floribunda* var. *isabellina.*

(6) *vert.* × *Kewensis*
maternal hybrids
Kewensis × a plant
1 plant only, near *floribunda.*

(7) A plant of *Kewensis* was tested for parthenogenesis. Very poor seed was obtained, only one germinated, giving a plant of *floribunda.*

Variation in Kewensis on self-fertilization.

As already stated, *P. Kewensis* on self-fertilization generally breeds true to type, but varies in some particulars, such as size, degree of hairiness, amount of meal, and flower colour.

Size. The variations in size are considerable, small plants occurring in the same families with large plants. The chromosomes of a small plant were counted by Miss Thomas, and were found to be 36 diploid and 18 haploid. Hence the number of chromosomes is not directly connected with the size of the plant.

Hairs. The F_1 hybrids possess short stalked glands visible with a lens, resembling those seen in *verticillata* when the meal is dissolved in alcohol. In succeeding generations occasional plants of *Kewensis* occur which have hairs on the leaves visible to the naked eye, and on microscopical examination these are seen to be glandular, the stalk much longer than in *verticillata*, but still generally not so long as the long hairs of *floribunda*, although an occasional hair may attain this length. (See p. 163, description of types.)

Mealiness. Pl. XXVIII, fig. 10. The inheritance of the different degrees of mealiness has been studied in some detail. Mealiness is not an easy character to analyse. The distribution of meal on the plant may vary, as well as the quantity, and there is further the difficulty occasioned by the fact that a plant which at the beginning of the season is only slightly mealy may become mealy all over at the end of the season. Therefore the degrees of development of this character only admit of a rough classification as follows:

(1) Meal distributed over the entire surface of the plant $= M^1$.

(2) Meal on the corolla tube, calyx and bracts, and slightly on the peduncles; or restricted to the nodes and calyx, and other intermediate forms $= M^2$.

(3) Meal only present inside calyx and on corolla tube $= M^3$. (Occasionally the meal of such plants is very slight in quantity.)

We find that M^1 throws M^1 only. One exception has been met with in a family of four plants; one of these was less mealy. This exceptional plant was not kept, and we do not know if it would have developed more meal later.

Plants classified as M^3 have sometimes thrown only M^3, but our numbers are too small to prove that M^3 can be fixed. They may throw all other forms.

The intermediate forms (M^2) are always heterozygous as far as our experience goes, and throw all forms.

Owing to the difficulty of classifying the plants, we know nothing of the number of factors involved. M^1 is evidently recessive to all the other forms.

Colour. In 1914 a new flower colour appeared in one of our *Kewensis* families, very much paler than any we had seen before. It apparently breeds true. We know nothing concerning the origin of the parent of the plant which had the new colour. But in 1915 the same colour appeared in the offspring of a cross between *Kewensis* and a plant with a complicated ancestry, no. $\frac{18}{12}$. The results obtained from this plant are peculiar, and will be the subject of a separate account.

Doubling. In Messrs Veitch's nursery a double variety has been obtained. The account of its origin is of some interest. A plant (Pl. XXVI, fig. 5) with single and double flowers appeared, the doubleness varying in degree. The double flowers were sterile, and the plant was propagated by division. By repeating the process of division, plants bearing only double flowers were obtained.

ORIGIN AND GENETIC BEHAVIOUR OF A NEW DIPLOID FORM EXHIBITING NORMAL SEGREGATION.

We now come to the most interesting case of segregation in *Kewensis.* In 1911 we received from Messrs Veitch two families of *Kewensis.*

A. Kewensis × *floribunda. F_1.* Five plants *Kewensis.*

Four of these plants were selfed; the seed of only one germinated, giving two plants, one of which died before being described. The other plant, no. $\frac{8}{12}$, differed from other *Kewensis* in having a less robust habit and long narrow ovate leaves.

B. Kewensis × *floribunda* var. *isabellina. F_1.* Nine plants *Kewensis.*

Seed from eight of these plants was sown; five gave no germination, one gave a large number of plants all *Kewensis*, and two gave a single plant each. One of these was ordinary *Kewensis*; the other, numbered $\frac{77}{12}$, was ordinary *Kewensis* in appearance, but behaved very differently genetically. Unfortunately the chromosomes of these plants were not counted. Their genetic behaviour will be described on p. 177.

Description of $\frac{18}{12}$. Pl. XXVI, fig. 4.

Plant less robust and smaller than *Kewensis*, very floriferous. Many superimposed whorls of flowers subtended by leafy bracts, erect flowering stems, about 18 inches, peduncles thin. Leaves narrow ovate covered with glandular hairs visible to the naked eye, varying in length from 1-celled stalked glands to 6-celled hairs with glands. Meal inside calyx and on corolla tube as in *Kewensis*, slight meal at nodes. Flowers large yellow, in size and colour as in *Kewensis*, but the petals not so imbricate, and flatter. The anthers at the mouth of the tube and the stigma at the same level; the anthers are usually shrivelled, when pollen is produced it is small in quantity, and examined microscopically only about 40 per cent. of the grains appear good. The average diameter of the grains is 5·6 μ, but there is great irregularity in size and shape.

The chromosomes of this plant were counted by Miss Digby, and found to be 18 diploid and 9 haploid in number. In this it resembles the original hybrid obtained at Kew, and this resemblance is borne out by the marked sterility which it exhibits[1]. When used as a female, either with its own pollen or with the pollen of other forms, this plant is excessively sterile, but its pollen used on *floribunda* is quite effective.

Self-fertilization has given the following results:

1912. 7 flowers selfed, gave 2 plants; 1 died before being described. 1 = $\frac{24}{13}$.

1913. Many flowers selfed, gave 1 plant = $\frac{202}{14}$.

1914. „ „ „ „ 2 plants; 1 died before being described. 1 = $\frac{49}{15}$.

All the plants resulting from the self-fertilization of $\frac{18}{12}$ differ from their parent and from one another; they have characters in common with the offspring of *floribunda* × $\frac{18}{12}$; they are smaller than the parent but vary in size, more or less hairy, never mealy, with yellow flowers. Three were thrums, and one pin. Of these plants:

$\frac{49}{15}$ has not yet been bred from.

$\frac{24}{13}$ and $\frac{202}{14}$ were perfectly fertile and gave a large number of plants varying much, and with characters in common with the offspring of *floribunda* × $\frac{18}{12}$. Those characters which exhibit a wide range of variation, such as size, leaf shape, degree of hairiness, and sterility, evidently depend on a large number of factors which makes them extremely

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[1] This plant was shown to Mr Coutts and Mr Garrett of Kew, who said that it resembled the sterile hybrid *Kewensis* first obtained at Kew.

difficult to analyse. No plant like $\frac{18}{12}$ appeared. These results are in accordance with those obtained from *floribunda* × $\frac{18}{12}$, to which we shall now pass.

P. floribunda × $\frac{18}{12}$.

We obtained five families from this cross. In four of these crosses the *floribunda* mothers used were from the cross *floribunda* × *verticillata*, and in the fifth cross a pure-bred *floribunda* was used. There was a general resemblance between the offspring of all these crosses.

The F_1 plants showed great variation, but all of them would be classed as *floribunda*-like plants. Characters which they all possess, and which are common to *floribunda*, are the small size, dimorphic flowers, hairiness, and absence of meal. In F_2 and F_3 the same general features were exhibited. The large size, the mealy character and the scented flowers of $\frac{18}{12}$, which may be supposed to come from *verticillata*, never reappeared in these families. The difficulty of classifying all the degrees of variation which occur for every character makes it impossible for us to do more than make a general statement. Evidently a very large number of factors are involved, and except in the case of colour we shall not attempt to give precise figures.

In size, habit, leaf and flower shape, and degree of hairiness, very great variation occurs. The smaller plants do not always breed true, even when derived from the larger. The habit may be flexuous or bending as in *floribunda*, or erect as in *verticillata*, but there is a wide range of intermediates, many of which are erect in the early stages of growth and flexuous later. At the time of flowering the plants may still be single-crowned rosettes, or they may have broken up into many-crowned tufts. The former plants have hitherto bred true to this character. The time of flowering and the length of the flowering period vary greatly, and there are numerous morphological differences connected with these characters. The leaves vary from long narrow ovate as in *verticillata* to broadly ovate, and may be pointed, rounded, or obovate at the tips. The length of the petiole varies also. The petals are stellate or imbricate, flat or reflexed or funnel shaped; the corolla tubes vary in length. The hairs range from very short glandular hairs approaching the *Kewensis* type of hair to long pointed hairs like those of *floribunda*.

Sterility.

The male sterility of $\frac{18}{12}$ reappears in many of the families from *floribunda* × $\frac{18}{12}$. In these families the anthers may contain very little pollen or occasionally no pollen. We have no evidence as to the inheritance of the female sterility which is so marked a feature of $\frac{18}{12}$. Cases in which no seed is produced could be equally well accounted for by deficiencies in the pollen.

It is a remarkable feature of this group of plants that, though $\frac{18}{12}$ gives little seed which rarely germinates, the seed of its derivatives germinates freely.

Dimorphic structure of the flowers.

The structure of the flowers of $\frac{18}{12}$ is like that of a thrum *floribunda*, in that the anthers are at the top of the corolla tube and the style is long, the stigma protruding beyond the anthers. The plant is heterozygous, giving thrums and pins on selfing and also on crossing with a *floribunda* which is heterozygous for these characters. Among the offspring of $\frac{18}{12}$ thrums and pins occur, but within these two forms are numerous minor variations affecting the position of the anthers and the length of the style. We have sometimes had difficulty in deciding whether a plant was thrum or pin by its appearance, for plants occur in which the anthers are only half-way up the tube and the style long. On breeding from these intermediate forms we have generally found that they were capable of throwing some pins with the anthers at the base of the tube, and we have therefore accepted them as thrums. Microscopical examination of the pollen gives little help in deciding whether a plant is thrum or pin, for the grains are very irregular in size and shape and many of them are bad. The pollen of pins is generally smaller than that of thrums, but in some pins grains as large as those of thrums occur.

We have found that the pins breed true except in one case which we regard as due to an error (p. 167): the thrums breed true or throw both forms. The ratio of thrums to pins varies somewhat in different families, but there seems little reason to suppose that the two forms are not members of a simple allelomorphic pair. The irregular numbers obtained are perhaps due to the sterility which exists in varying degrees in all the families derived from $\frac{18}{12}$ and its crosses.

Flower colour. The two flower colours yellow and isabellina occur in various shades. Besides these, a new yellow colour has appeared which we have called lemon. It is very near the pale yellow of certain strains of *verticillata* but as a rule differs from these in that the margins of the petals are darker. Before giving the more complicated experiments in which the lemon colour is involved, we will consider our records of the inheritance of yellow and isabellina (taken from various families and not confined to the descendants of $\frac{18}{12}$).

From heterozygous yellow plants selfed the total numbers are *yellow* 518 : *isabellina* 208. From heterozygous yellow × isabellina and the reciprocal cross, the total numbers are *yellow* 142 : *isabellina* 159.

The numbers from which these totals are compiled are irregular. Among 36 yellow plants selfed, the proportion of yellow : isabellina varies from 10 yellow : 14 isabellina to 13 yellow : 1 isabellina. We have not observed any relationship between the colour factor and the factor for heterostyly. In those families derived from plants heterozygous for yellow and thrum, the total numbers are:

Yellow thrum 135 : yellow pin 33.
Isabellina „ 32 : isabellina „ 17.

In spite of the irregular numbers, there seems no reason to doubt that yellow and isabellina are a simple allelomorphic pair.

The results of all the crosses with $\frac{18}{12}$ will now be given.

$$\frac{31}{12}\begin{bmatrix} F_1\ \textit{flor.} \times \textit{vert.} \\ \text{homozygous yellow} \end{bmatrix} \times \frac{18}{12}.$$

F_1. 26 plants all yellow.

Of these 13 plants were bred from. Twelve gave yellows only; one plant gave

28 yellow as in *floribunda*.
2 dark yellow as in $\frac{18}{12}$.
9 pale yellow.
1 lemon.

$$\frac{37}{12}\begin{bmatrix} F_1\ \textit{flor.} \times \textit{vert.} \\ \text{heterozygous yellow} \end{bmatrix} \times \frac{18}{12}.$$

F_1. 28 plants all yellow.

Of these 9 plants were bred from. Four gave yellows only. Four gave yellows and isabellina, the total numbers being 45 yellow: 18 isabellina. One ($\frac{56}{14}$) gave

24 yellow.
6 lemon.
7 isabellina.

$$\frac{32}{12}\begin{bmatrix} F_1\ \textit{flor.} \times \textit{vert.} \\ \text{heterozygous yellow} \end{bmatrix} \times \frac{18}{12}.$$

$F_1 = 5$ yellow : 2 isabellina.

Two yellow plants were bred from and gave yellows only.

Certain F_2 plants from the above crosses were bred from and gave the following results:

Lemons selfed.

$\frac{37}{14}$ ex $\frac{31 \times 18}{12}$ gave 2 lemon, like parent.

$\frac{54}{14}$ ex $\frac{37 \times 18}{12}$ gave 26 lemon: 5 isabellina.

$\frac{55}{14}$ ex $\frac{37 \times 18}{12}$ gave 26 lemon, dark and pale shades.

Yellows heterozygous for lemon and isabellina selfed.

$\frac{53}{14}$ ex $\frac{37 \times 18}{12}$	gave 7 yellow:	9 lemon:	5 isabellina.
$\frac{52}{14}$ ex $\frac{37 \times 18}{12}$	„ 9 „	5 „	6 „
Totals	16	14	11

$\frac{51}{14}$ ex $\frac{37 \times 18}{12}$ gave 10 pale yellow and lemon (not recorded separately) and 3 isabellina.

The following crosses were made among the F_1 and F_2 plants.

$\frac{56 \times 50}{14}$ Yellow F_1 (heterozygous for lemon and isabellina) x isabellina F_2.

13 yellow: 12 lemon: 17 isabellina.

$\frac{51 \times 55}{14}$ Yellow F_2 (heterozygous for lemon and isabellina) x lemon F_2.

25 yellow: 16 lemon.

$\frac{59 \times 50}{14}$ Yellow F_2 (heterozygous for lemon) x isabellina F_2.

8 yellow: 5 lemon.

We are not at present in a position to interpret these numbers. It seems probable that two pairs of factors are involved, but our numbers are small and irregular, and we must await the results of crossing lemon with isabellina to prove the correctness of this hypothesis.

P. Kewensis × $\frac{18}{12}$.

Many attempts to cross $\frac{18}{12}$ with *Kewensis* have been made, but these crosses have generally failed. We will now give the details of a cross of this nature which gave a single fertile plant. Unfortunately we have not been able to count the chromosomes of this plant or of its offspring. In 1915 a few hybrids of $\frac{18}{12}$ × *Kewensis* have been obtained, and we hope to continue the investigation of these hybrids, especially with regard to the inheritance of the number of chromosomes.

All attempts to cross $\frac{18}{12}$ with *verticillata* have failed.

In 1912 *Kewensis* $\frac{68}{12}$ [F_2 ex *Kewensis* × *flor.* var. *is.*] was fertilized by $\frac{18}{12}$, and gave one plant $\frac{66}{13}$, which resembled *Kewensis* but was not very robust. This plant was self-fertilized, giving 20 plants of *Kewensis*, differing from each other only as regards size. Two of the larger plants were selfed and gave *Kewensis*, but two of the smaller plants on selfing behaved differently. One such plant gave only two very small plants with leaves not more than two inches long: both had somewhat hairy leaves and meal in the calyx. The sister plant gave 5 plants, 4 of which had also somewhat hairy leaves and meal in the calyx, but 1 had hairy leaves and *no meal*. This plant also differed from the sister plants in being pin-eyed. Hence it came near *floribunda* type. The plant $\frac{66}{13}$ [F_1 ex *Kewensis* × $\frac{18}{12}$] was crossed back with $\frac{18}{12}$, and gave two plants, one of which was typical *Kewensis*; the other was small, with somewhat hairy leaves and meal in the calyx. On selfing this plant gave 6 plants all very near the parent plant[1]. The reciprocal cross, in which $\frac{18}{12}$ was used as a female with $\frac{66}{13}$ as male, gave one plant, near *floribunda* in type but with lemon coloured flowers.

Although these results are slight, still they give evidence that segregation occurs in the offspring of *Kewensis* × $\frac{18}{12}$, giving plants in which meal inside the calyx is combined with a considerable degree of hairiness on other parts of the plant, and finally a single plant near *floribunda* in type.

These results (except that of the reciprocal cross on $\frac{18}{12}$) are tabulated below.

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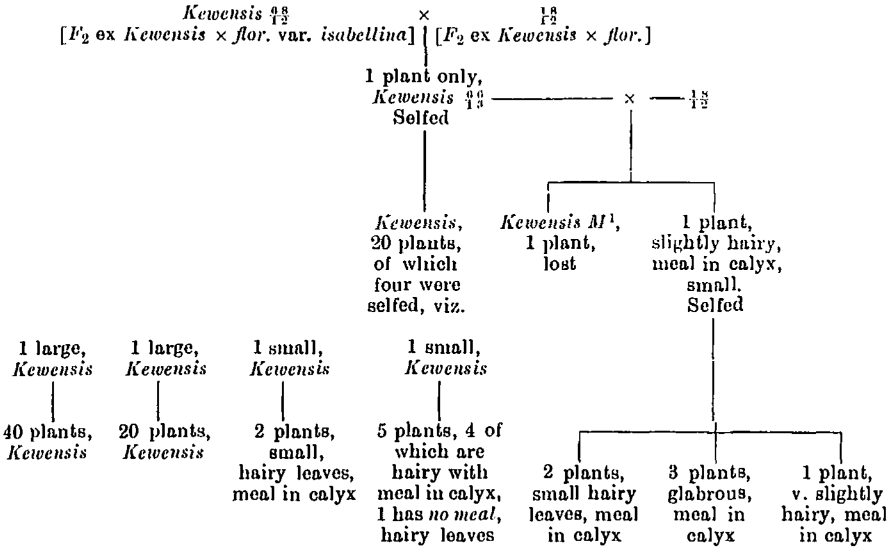
[1] The following result obtained this year gives further evidence as to the consequences of crossing the tetraploid with the diploid form. One of the 6 plants mentioned above, derived from such an original cross, selfed gave 13 *Kewensis* (not yet in flower) and 2 *hairy* plants with *lemon* flowers, thus showing that the power of segregation is now introduced. December, 1915.



We will now give details of another case of segregation in *Kewensis* (see p. 170).

P. Kewensis $\frac{77}{12}$ was, as already stated, typical *Kewensis* in appearance, except that the anthers were not quite at the top of the corolla tube, and the styles were shorter than is usual. There was much bad pollen. We lost the plant before we knew that there was anything exceptional in its behaviour. Self-fertilized this plant gave two plants, nos. $\frac{3}{13}$ and $\frac{79}{13}$.

$\frac{3}{13}$. Smaller plant than *Kewensis*. Leaves broadly ovate. Whole plant covered with hairs, visible to the naked eye but short and glandular. No meal. Flowers pale yellow, small, flat and imbricate. *Thrum*. Robust habit.

$\frac{79}{13}$. Small plant, flower stems only 6 inches high. Leaves narrow ovate (as in *verticillata*) but only 3 inches long. Hairs as in $\frac{3}{13}$. Flowers pale yellow, small, funnel-shaped. *Pin*.

Both these plants were selfed; the seed of $\frac{3}{13}$ failed to germinate in 1913, but selfed again in 1914 it gave

6 yellow thrum : 1 yellow pin.
3 isabellina thrum : 2 isabellina pin.

These plants varied from slightly hairy to moderately hairy.

On selfing, $\frac{79}{13}$ gave yellows and isabellina in the numbers 43 : 13. The yellows were pale in tint and there were two shades of isabellina.

All the plants were small flowered, pin, and all had a neat bushy habit with erect flower stems crowded together, the pedicels often sloping upwards instead of standing out at right angles to the main stem. Eleven of the plants had funnel-shaped flowers, and the rest flat stellate flowers. The size of these plants varied much, the internodes of one of the smallest measuring about $\frac{1}{2}$ inch, and of one of the tallest about 1 inch. It was remarkable that not one of these plants had leaves like the parent: they varied from ovate to broadly ovate.

Reciprocal crosses between $\frac{79}{13}$ and $\frac{3}{13}$ were made, and gave a total of

32 yellow thrums : 15 yellow pins.

2 isabellina thrums : 7 isabellina pins.

The results of these crosses as regards other characters are difficult to analyze; one plant only was obtained with narrow ovate leaves as in $\frac{79}{13}$. Two plants with weak stems and straggling habit appeared; as $\frac{79}{13}$ threw only erect bushy plants we must suppose that $\frac{3}{13}$ was heterozygous as regards habit.

Two crosses were made between $\frac{3}{13}$ and *Kewensis*, both of which failed.

Recapitulation of the foregoing section.

The two plants $\frac{18}{12}$ and $\frac{77}{12}$, both of which descend from the cross *Kewensis* × *floribunda*, exhibit in their offspring and descendants a wide range of variation. These forms possess characters derived from the original parent forms *verticillata* and *floribunda*, but they bear a stronger resemblance to *floribunda* than to *verticillata* or *Kewensis*. Thus in size, absence of meal, presence of hairs, and heterostyly, are seen evidences of *floribunda* influence which are common to all the plants, whereas in habit of growth, leaf shape, flower shape, and colour, the influence of either species may be seen. The recombination of parental factors occurs also as the result of crossing *Kewensis* with $\frac{18}{12}$, when the *floribunda* type has reappeared. It appears that in $\frac{18}{12}$ we have a plant which forms a link between *floribunda* and *Kewensis*, by which characters from both forms may be recombined. The barrier that prevents the recombination of certain *verticillata* characters, such as size and habit, with the full degree of hairiness of *floribunda*, may perhaps break down in the offspring of $\frac{18}{12}$ × *Kewensis*.

P. KEWENSIS COMPARED WITH OTHER TETRAPLOIDS.

The genetics of two other tetraploid forms, viz. *Œnothera gigas*[1] and *Primula sinensis*[2], have been studied. Neither of these tetraploids arose as the result of crossing two species, and therefore they are not parallel cases with *Kewensis*, still it is of some interest to compare them.

Although these three tetraploid forms are alike in possessing double the number of chromosomes of the types from which they come, we do not know if they resemble each other as regards the comparative size of the chromosomes. As shown by Farmer and Digby[3], " the total amount of chromosome substance in the nuclei of each of the two types of hybrids known as *P. Kewensis* is the same. The nuclei of the one form of hybrid contain twice as many chromosomes as the nuclei of the other type, but the increase in number is associated with a corresponding diminution in size." Although the size of the chromosomes in the tetraploid is thus diminished, the size of the nuclei and cells are larger than in the diploid. In their discussion of these facts, Farmer and Digby conclude that the doubled number of chromosomes may be attributed to a transverse fission of the "normal" chromosomes. They suggest that the increase in size of nuclei and cells may be due to a correlation between these sizes and the superficial area of the chromosomes, for the transverse fission of the chromosomes would add to the normal amount of free surface. The volume of the chromosomes in *Œ. gigas* and in the tetraploid *P. sinensis* have not been determined, but another giant form of *P. sinensis* has been investigated by Gregory[4]. This giant was found to have the diploid number of chromosomes, but nuclei and cells larger than in the normal form.

It remains to consider to what extent the doubling in the number of chromosomes is correlated with an increase in the size of the plants. In the case of *Œ. gigas* the evidence is not perfectly consistent, the work of Geerts and Stomps, and that of Miss Lutz, giving different results. Heribert-Nilsson[5] (refs. given) concludes that the doubling of the chromosome number is not the primary cause of the peculiar habit of *gigas*. In the tetraploid form of *P. sinensis* the correlation

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[1] H. de Vries, *Gruppenweise Artbildung*, 1913.

[2] R. P. Gregory, *Proc. R. S.*, B. 87, 597.

[3] Farmer and Digby, *Phil. Trans. R. S.*, B. 205.

[4] R. P. Gregory, *Proc. Camb. Phil. Soc.* Vol. xv. Part III. p. 239.

[5] N. Heribert-Nilsson. *Spaltungserscheinungen der Œnothera Lamarckiana*, 1915 Lunds Universitets Årskrift.

between size and chromosome number appears definite, but in the diploid giant there is a general increase in size without a doubling of the chromosome number. In *Kewensis* the tetraploid varies considerably in size, the small plants being no larger than the diploid form; the chromosomes of one of these small plants were counted by Miss Thomas, and were found to be 36 diploid number, 18 haploid number. It is doubtful whether the tetraploid attains a greater size than well-grown plants of *verticillata,* certainly not greater than might be accounted for by the increase of vigour often seen in hybrids. It is desirable that further chromosome counts should be made, meanwhile we must assume that number of chromosomes is not directly associated with the size of plant.

In the tetraploid *P. sinensis,* Gregory found that the factorial system is doubled, while in the diploid giant this is not so. We cannot say if the tetraploid *Kewensis* possesses a doubled factorial system, for we have no diploid form with which to compare it. The only characters which exhibit anything like normal segregation in *Kewensis* are the various degrees of mealiness, and the phenomena met with in the inheritance of these characters might be equally well accounted for by the doubling of a few pairs of factors or by the presence of several factors.

In *P. sinensis* fertilization cannot be effected between the tetraploid and diploid forms, but in *Kewensis* this is not the case.

The genetic behaviour of *Œ. gigas* exhibits certain puzzling features. Dwarf forms are thrown by it in the proportion of 40 per cent., but we are not told if these are diploid or tetraploid. A narrow-leaved form appears but de Vries considers the leaf breadth to be a fluctuating character. Crosses between *gigas* and other forms have given various results in the hands of different workers. It seems probable that individual plants differ in their genetic constitution, in spite of the fact that they breed true to *gigas* on self-fertilization. (For summary of facts and discussion see Heribert-Nilsson[1].)

SUMMARY.

I. From the cross *P. verticillata* by *floribunda* and the reciprocal, plants resembling the female parent are generally obtained. Their origin as the result of parthenogenesis cannot be held to be disproved, but these maternal hybrids rarely show any evidence of segregation when used for crossing, and usually on self-fertilization breed true to type.

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[1] N. Heribert-Nilsson. *Spaltungserscheinungen der Œnothera Lamarckiana*, 1915.

II. Occasionally hybrids of the form known as *P. Kewensis* are obtained. These are of two kinds, one partially sterile, having the diploid number 18 chromosomes, the haploid number 9 chromosomes, the other fertile and having 36 and 18 chromosomes respectively.

III. The hybrids whether maternal or otherwise are obtained in very small numbers, and although F_1 seed which appears good is often formed, great difficulty in germinating it is met with. Uncertain germination is however common in these plants.

IV. *P. Kewensis* self-fertilized generally breeds true to type, segregating only in certain factors such as degree of mealiness and flower colour; when crossed with parent types it commonly produces maternal hybrids, but in rare cases gives evidence of segregation.

V. The genetic behaviour of two plants of *Kewensis*, bred from *Kewensis* [F_1 *Kewensis* × *floribunda*], received from Messrs Veitch in 1911, was however peculiar. The offspring of these plants did not resemble *Kewensis*, but approached nearer to *floribunda*. One of them was found to have 18 diploid and 9 haploid numbers of chromosomes, and this plant exhibited segregation, giving new forms representing recombinations of *floribunda* and *verticillata* characters. These plants are also peculiar in that their seed germinates freely.

VI. Among these new forms are many shades of yellow not previously known in these plants. When we began our work, the only colours known were the full yellow of *floribunda* type and of *Kewensis*, the paler yellow of *verticillata*, and the pale cream yellow of the variety of *floribunda* known as *isabellina*. The full yellow and the pale isabellina shade evidently depend on a factorial difference, the full yellow being a dominant. The numbers given have however a wide range of irregularity. The factorial inter-relations of the new colours have not yet been sufficiently investigated.

VII. The diploid plant which thus exhibits segregation has also been crossed successfully with *Kewensis* tetraploid. From this cross plants intermediate between *floribunda* and *Kewensis* have arisen, and also a few plants resembling *floribunda*.

DESCRIPTION OF PLATES.

PLATE XXV.

Fig. 1. *Primula floribunda.*
Fig. 2. *P. verticillata.*
Fig. 3. *P. floribunda* × *verticillata.* The diploid F_1, first obtained at Kew. Figure kindly supplied by Sir Harry Veitch.

PLATE XXVI.

Fig. 4. The plant numbered $\frac{18}{12}$. See text.
Fig. 5. *P. Kewensis*, tetraploid, with some double flowers; seen at Messrs Veitch's.

PLATE XXVII.

Fig. 6. Leaf of *P. verticillata.*
Fig. 7. Leaf of *P. floribunda.* Note the hairs.
Fig. 8. Leaf of *P. Kewensis*, diploid.

PLATE XXVIII.

Fig. 9. Leaf of *P. Kewensis*, tetraploid.
Fig. 10. Leaf of ditto, mealy variety.
Fig. 11. Leaf of $\frac{18}{12}$.

The leaves are all shown as seen from the dorsal surface.

PLATE XXIX.

Figs. 12—16 show the series of colours which occur among the derivatives of the cross *floribunda* × $\frac{18}{12}$.

Fig. 12. Light isabellina.
Fig. 13. Isabellina.
Fig. 14. Lemon.
Fig. 15. Light yellow.
Fig. 16. Dark yellow.
Fig. 17. Diploid *Kewensis.*

The coloured drawings represented in these Plates were made by Mr Osterstock from the plants. The reproductions are fairly accurate, but in the originals the distinctions between the colour-varieties are somewhat more pronounced.

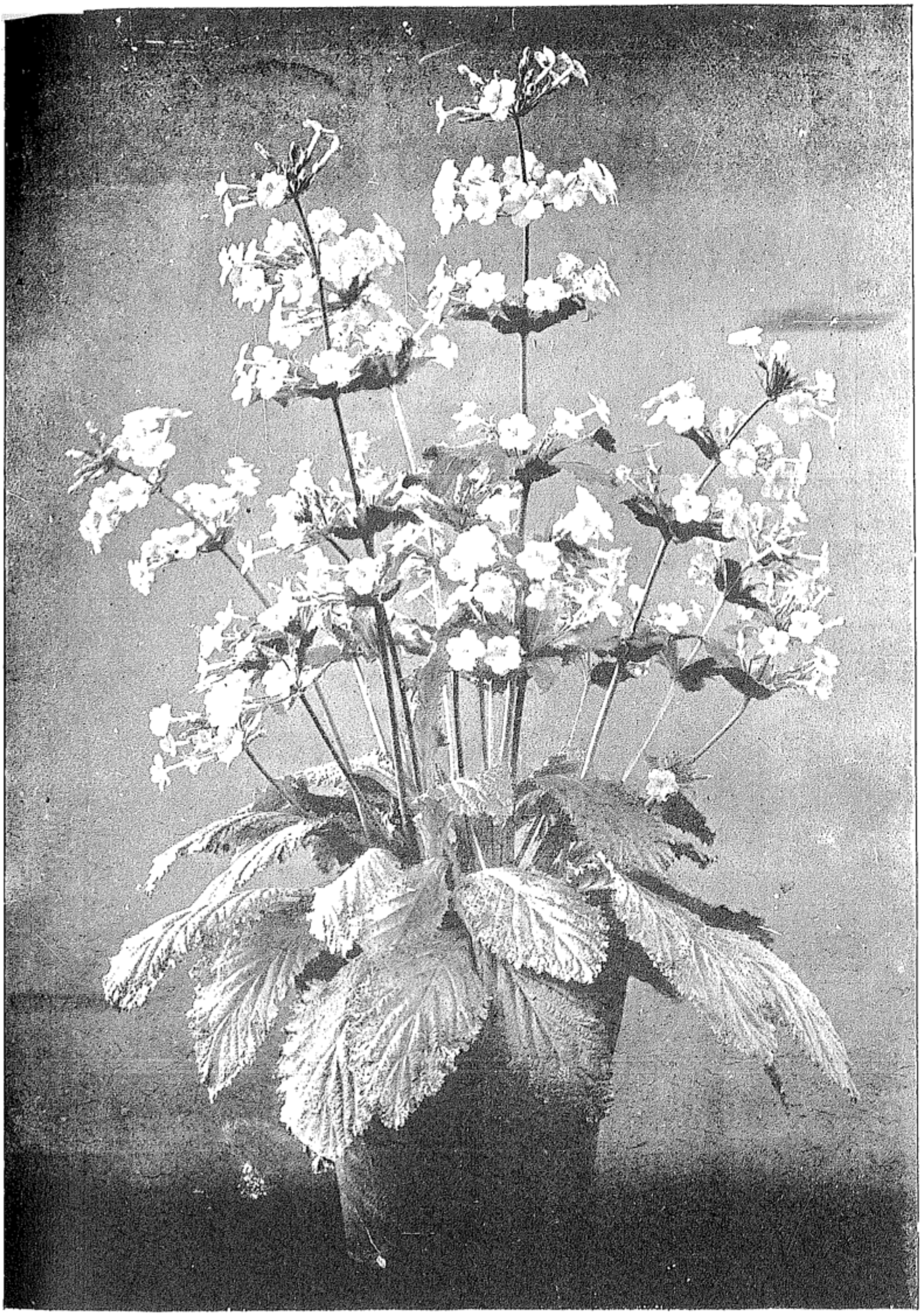


Fig. 3.

Fig. 4.

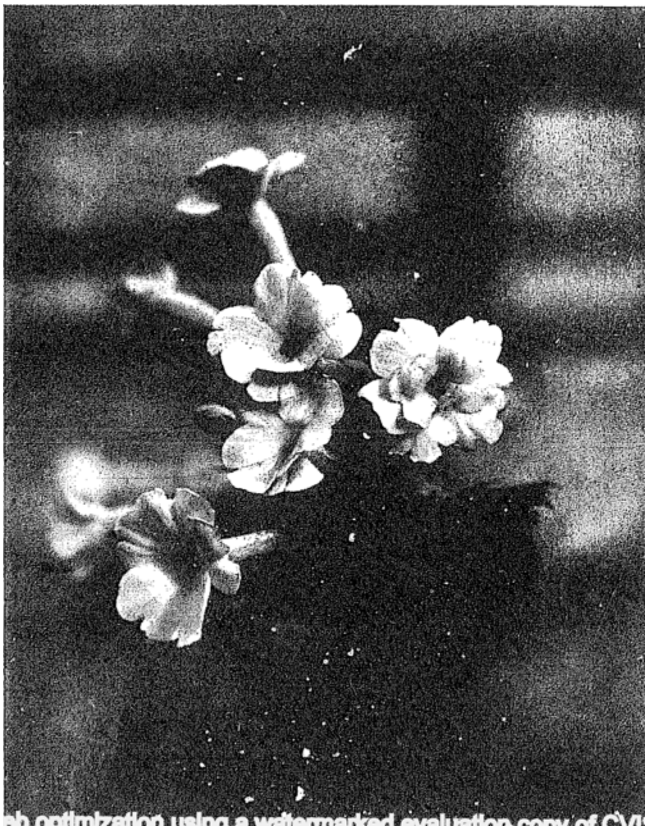


Fig. 5.

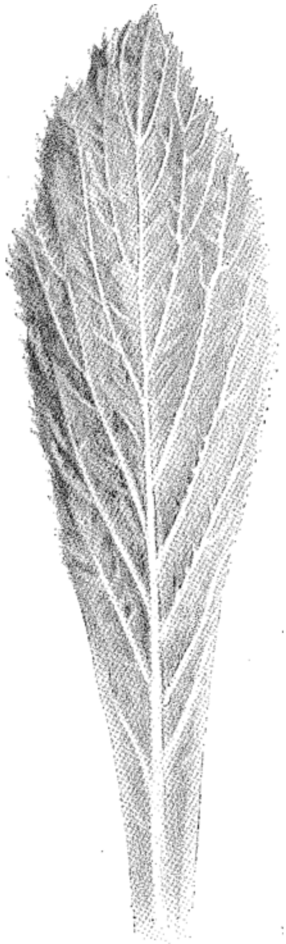


Fig. 6.

Fig. 8.

Fig. 7.

Fig. 9.

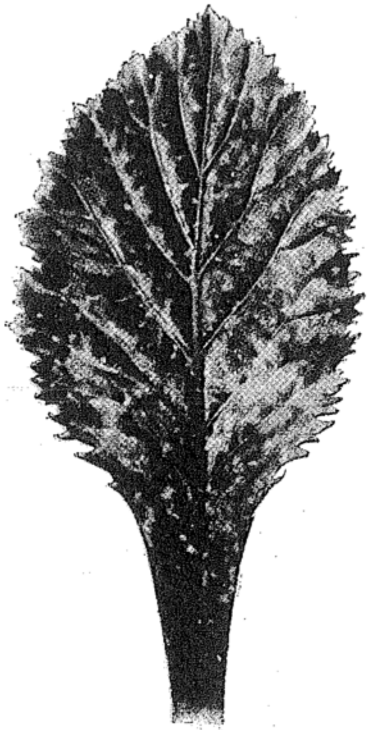
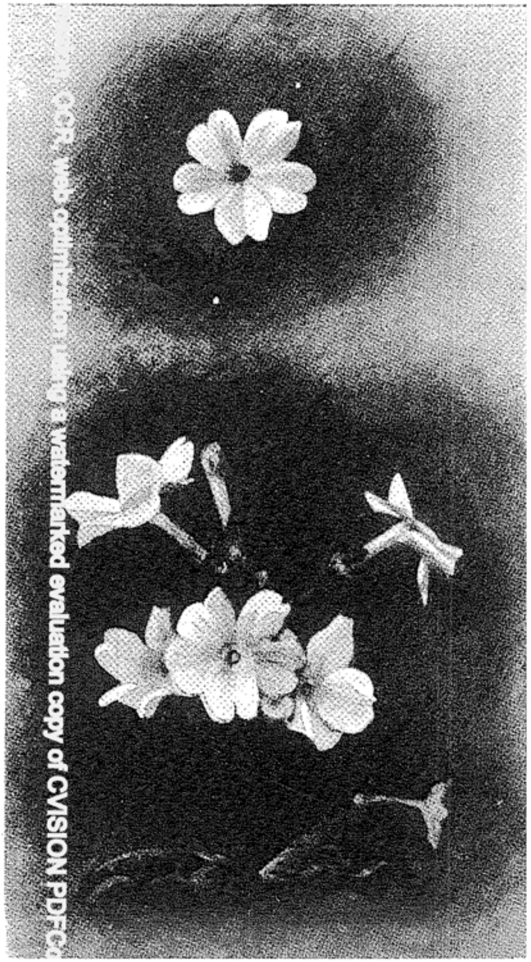


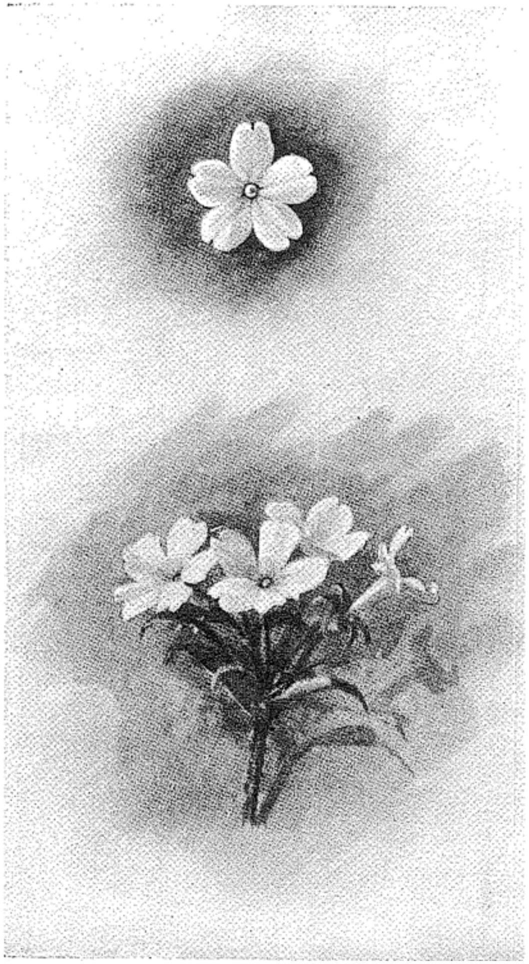
Fig. 10.

Fig. 11.



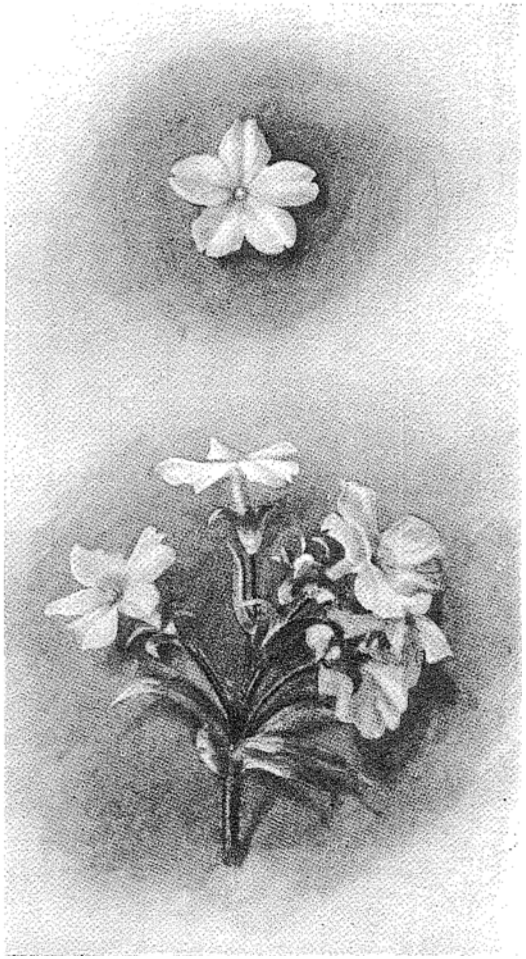
Light isabellina.

Fig. 12.



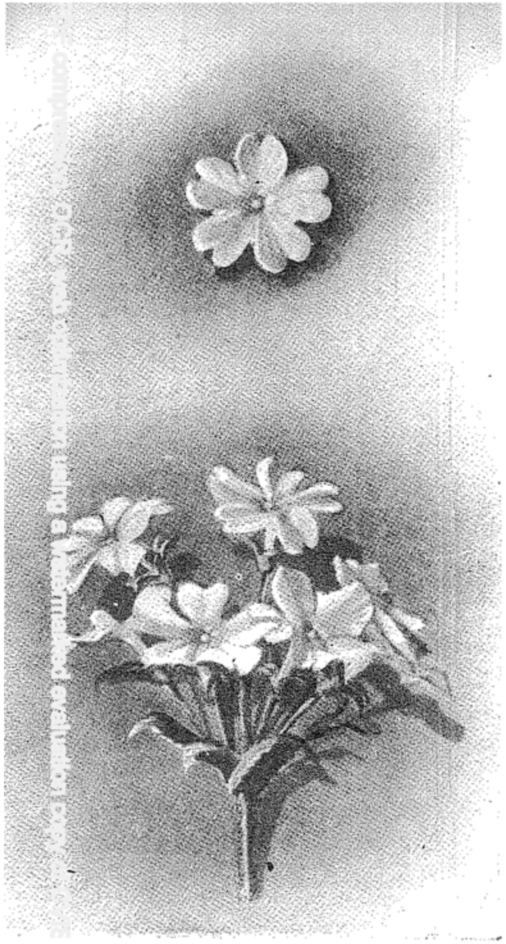
Isabellina.

Fig. 13.



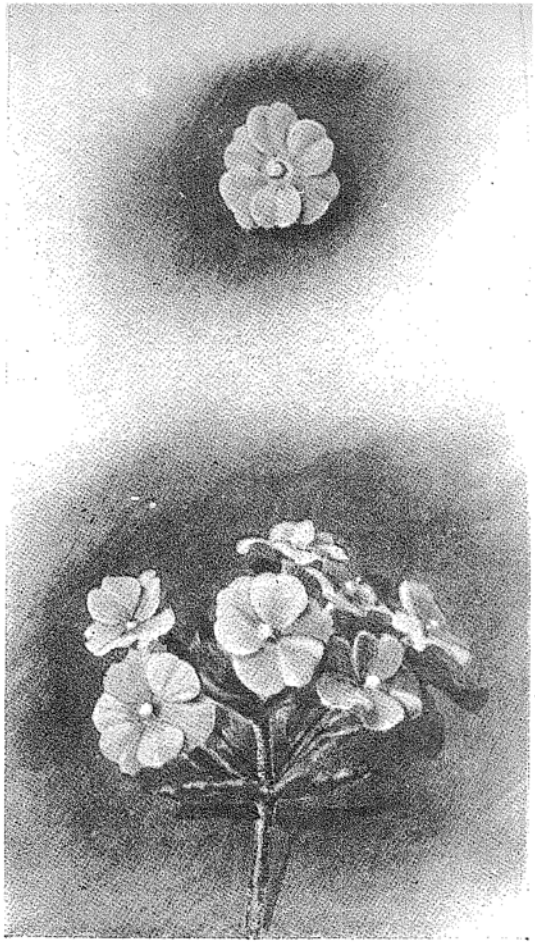
Lemon.

Fig. 14.



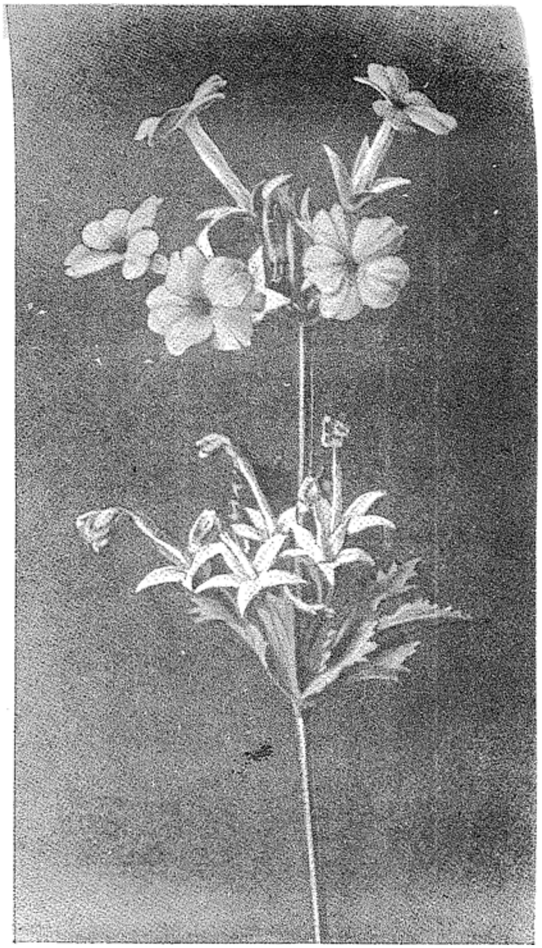
Light yellow.

Fig. 15.



Dark yellow.

Fig. 16.



Yellow. Diploid *Kewensis.*

Fig. 17.

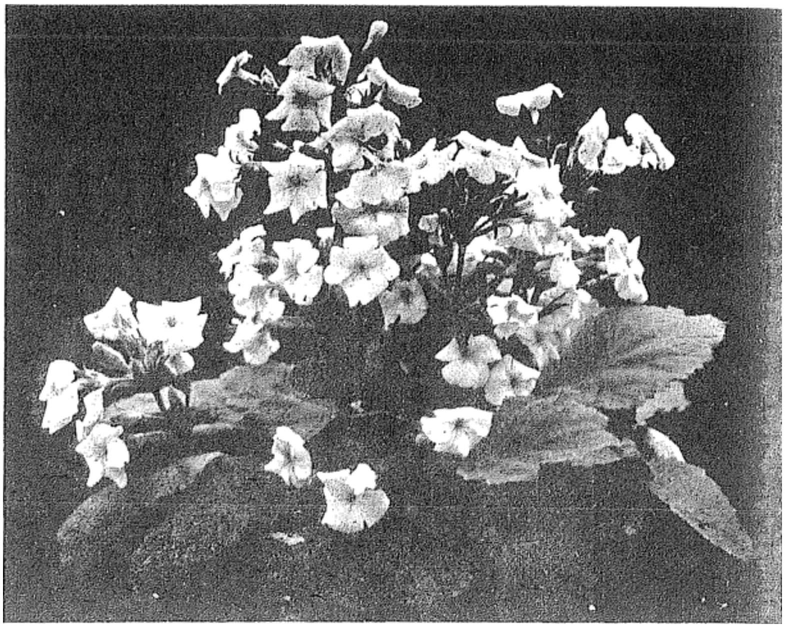


Fig. 1.

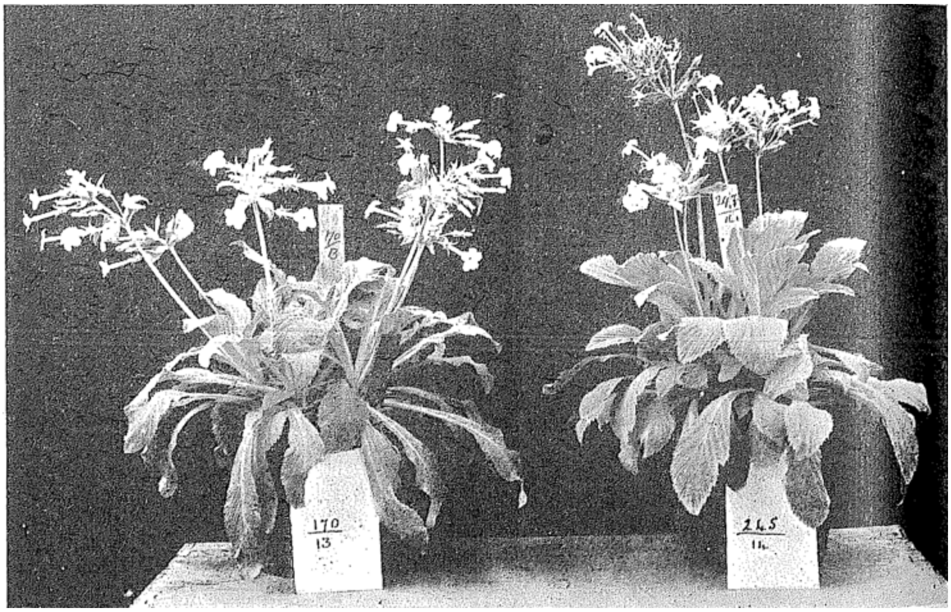


Fig. 2.

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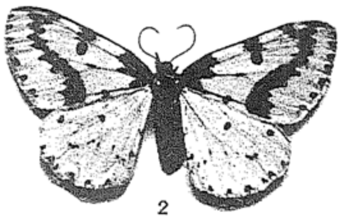
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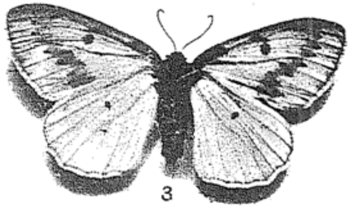
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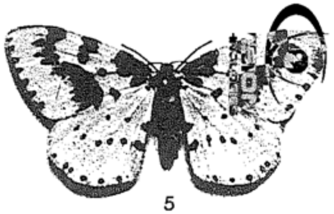
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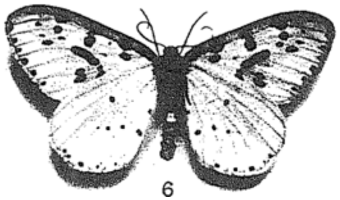
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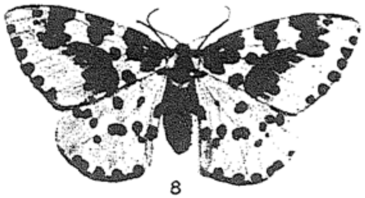
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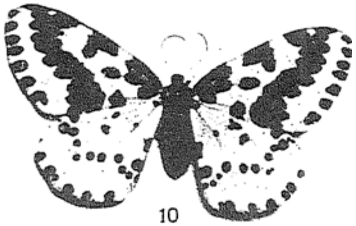
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