# GENETICAL AND CYTOLOGICAL STUDIES IN THE GENUS SOLANUM.

By H. C. Choudhuri, B.A., M.A. (Cal.), Ph.D.(Lond.)

Thesis presented for the Degree
of Doctor of Philosophy,
Edinburgh University.

NOVEMBER, 1942

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## 1. INTRODUCTION.

Previous studies on the cytology of wild and less well-developed "diploid" forms of potatoes have been mainly concerned with the number of chromosomes: this number has proved to be a strictly constant specific character. These studies have been undertaken usually in the hope that they would throw light on the phylogeny, and interrelationship of the various forms of specific and subspecific rank, and elucidate their breeding possibilities. Rybin (1933) in his cytological investigation on the South American cultivated and wild potatoes has recorded twelve as the haploid number of chromosomes in seven species, including Solanum Rybinii. Ratera (1938) determined the same number of haploid chromosomes in S. Parodii and six other species indigenous to Argentine.

Artificial interspecific hybrids of "diploid" potatoes have been recorded from time-to-time by various authors, e.g. Bukasov (1938), Emme (1936), Schwartz and Kuzmin (1936) and Krasnyi Pakhar (1935) etc. These authors gave little if any attention to the chromosome number of their plants but rather concentrated on the inheritance of flower colour, resistance to diseases or the genetical sequelae to exposure to low temperature, all in connection with the possible utilisation of the plants in commerce.

The present study is concerned primarily with the behaviour of the chromosomes and their secondary associations at meiosis in six "diploid" species with a view to determine the much discussed basic number in the potatoes. So far investigation of this type has dealt only with the commercial varieties of *Solanum tuberosum* L., (Ellison 1935) and its "diploid and triploid representatives" (Müntzing 1933), on the basis of the recent interpretation of secondary association of chromosomes. Special attention has also been given here to two interspecific hybrids to determine the homology of their chromosomes.

The plants studied were:-

| Ref. No. | Species and hybrids | Origin | Wild = W. Native-cultivated = N.C. | Flower colour |
|---|---|---|---|---|
| *E.P.C.40 | *Solanum lanciforme* Rydb. | Mexico | W. | Yellowish-white. |
| " 84 | *S.Parodii* sp. coll. Juz. et Buk. | N.Argentine | W. | White |
| " 85 | *S.infundibuliforme* Phil. | N.Argentine | W. | Pale mauve. |
| " 1104 | *S.stenotomum* var. Juz. et Buk. | Peru | N.C. | Blue-purple. |
| - | *S.Rybinii* Juz. et Buk. | Colombia | N.C. | Tinted white.ø |
| - | *S.polyadenium* Greenman | Mexico | W. | White |
| + 1028d/3 | *S.Parodii* x *infundibuliforme* | | -. | |
| + 993a/3 | *S.simplicifolium* Bitt. x *Rybinii* | | - | |

* Empire Potato Collection Expedition Reference Number.
\+ Scottish Society for Research in Plant Breeding Reference Number.
ø Reddish-purple tinge on the apex of under surface.

## 2. MATERIAL AND METHODS.

All the material was grown at the potato station of the Scottish Society for Research in Plant Breeding, Boghall, Midlothian, during the summer of 1941.

The meiotic division in pollen-mother-cells begins when the anther is comparatively small. Aceto-carmine was used to determine the stages at which the buds were ready for fixation. All buds were pretreated in

Carnoy's fluid (6:3:1) for 4-7 seconds (Kihara's method, vide La Cour 1931). Such pretreatment for more than 7 seconds had a deleterious effect on the cytoplasm. Various other fixing fluids were tried including Strong Flemming, La Cour's fixative 2BD and the fixative due to Navashin made up as:

I. Chromic acid - 1 gm. )
Acetic acid (concentrated) - 10 cc. )
Distilled water - 85 cc. ) Vide
) Müntzing
II. Formalin 40% - 30 cc. ) 1933.
Alcohol 95% - 10 cc. )
Distilled water - 55 cc. )

(At the time of fixing equal parts of I and II were mixed.)

Generally the best results were obtained by using this Navashin fixative. Strong Flemming gave results equally good but Navashin proved to have some advantages and was employed exclusively in all later work.

In the case of material from fixatives containing osmic acid, sections were bleached overnight in a solution of Hydrogen-peroxide (1 part 20 vol. $H_2O_2$ to 3 parts of 80 per cent alcohol). Staining was by Newton's Gentian-violet-iodine technique, and where difficulty occurred an aqueous solution of 1 per cent chromic acid was employed as a mordant as recommended by La Cour (1931).

## 3. TAPETUM.

An important feature of the tapetum is that the tapetal cells become binucleate prior to the time when the pollen-mother-cells are at pachytene and generally remain so during the whole period of pollen formation. Interspersed among the binucleate cells a number of uni-nucleate cells may remain. In a number of tapetal cells division of the nuclei may be carried further, and results in three- or four-nucleate cells.

Very frequently tapetal cells project into and even reach across the loculus, thus cutting it into several compartments. Often this tissue seems to occlude a group of pollen-mother-cells which appear immersed in the tissue of tapetal origin. Similar behaviour of tapetal tissue has been referred to by Clausen (1926) in *Viola* hybrids and by Meurman (1928) in sterile *Ribes Gordonianum*. Both these authors concluded that this phenomenon was correlated with the nutrition of the developing pollen.

Cells with high number of chromosomes, although rare, have been noted in tapetal tissue. Fig. 1 drawn from a tapetal tissue shows as many as 48 chromosomes; this may have been due either to failure of the spindle mechanism or amalgamation of two nuclei. Levan (1938) in his study of the behaviour of colchicine treated root tips of *Allium* recorded cells with very high chromosome number which the author regarded as being due to the failure of the spindle mechanism.

At later stages the tapetum undergoes great elongation in the direction of the long axis of the anther, and finally appears at the time the pollen lies free as a thin layer.

## 4. MEIOSIS IN POLLEN-MOTHER-CELLS.

Early (pre-diakinetic) stages of meiotic division were not suitable for critical studies in all the species under consideration owing to difficulties of fixation, although in S. Rybinii and S. Parodii a few nuclei at pachytene were found which were well fixed. Owing to the lack of material critical examination could not be made of this stage of division.

Along with normally dividing pollen-mother-cells there appeared a certain number of distorted and probably enucleate individuals which appeared as deep-stained undifferentiated masses. Frankel (1940) working with species of Hebe reported in all cases a certain amount of degeneration of pollen-mother-cells either at pachytene or in subsequent stages of pollen development. The stage at which degeneration occurs, he found to be characteristic for each form of Hebe.

### (a) First and Second Division in Species.

### I. S. lanciforme Rydb.

At diakinesis twelve bivalents are observed. The chromosomes here are either held by a single terminal association or by two terminal chiasmata one at either end, and in this case forming ring bivalents (Fig. 4).

At metaphase as might be expected from diakinesis generally 12 bivalents are seen (Fig. 8). Figure 5 shows a side view of metaphase with ring and rod bivalents. 13 chromosomes were occasionally observed in polar view owing presumably to the presence of 11 bivalents and 2 univalents (Fig. 6, u); this had been easy to follow at side view where univalents failed to orientate on the equatorial plate. A metaphase complex is drawn separately to show 11 bivalents and 2 univalents (Fig. 7, u). Table I shows the frequency of univalents in 539 pollen-mother-cells.

TABLE I.

Chromosome complement at first metaphase in 539 pollen-mother-cells of S. lanciforme.

| Metaphase complement | Frequency | Figure |
|---|---|---|
| 12 bivalents | 527 | 5 |
| 11 bivalents and 2 univalents | 12 | 7 |
| Total P.M.C.*analysed | 539 | |

* P.M.C. = pollen-mother-cells.

Association of chromosomes quite distinct from the primary or prophase pairing, generally known as secondary pairing or association was observed and was very conspicuous in the polar view of metaphase. Various types of associations are shown in Table II and Figs. 9-19.

TABLE II.

Showing character and frequency of secondary associations at first metaphase in S. lanciforme.

| Number of single bivalents | No. of bivalents in groups of | | | Frequency | Figure |
|---|---|---|---|---|---|
| | 2 | 3 | 4 | | |
| 12 | - | - | - | 15 | 8 |
| 10 | 1 | - | - | 12 | 9 |
| 9 | - | 1 | - | 6 | 10 |
| 8 | 2 | - | - | 24 | 11 |
| 8 | - | - | 1 | 1 | 12 |
| 7 | 1 | 1 | - | 11 | 13 |
| 6 | 3 | - | - | 26 | 14 |
| 6 | - | 2 | - | 2 | 15 |
| 5 | 2 | 1 | - | 4 | 16 |
| 5 | - | 1 | 1 | 1 | 17 |
| 4 | 4 | - | - | 31 | 18 |
| 4 | 1 | 2 | - | 3 | 19 |
| Total P.M.C. analysed | | | | 136 | |

At early anaphase the bivalents disjoin and move towards the poles, while univalents which had failed to orientate on the metaphase plate hardly show any indication of movement at this time. In Fig. 20 two univalents (u) are shown which lie on one side of the equatorial plate, here the chromosomes are drawn separately to show the separation of the rest of the

11 chromosomes towards their respective poles.

In late anaphase the bivalents are seen to lag between the two poles. The behaviour of univalents during division is variable (Table III). They may split while lagging, and the variable number of univalents on the divisional plane seems to be due to some of the univalents reaching a pole divided or undivided while the rest lag or are eliminated (Figs. 23-26). This will lead to unequal distribution of chromosomes to the poles. The presence of 10 and 11 chromosomes on opposite sides of the equatorial plate with one univalent eliminated and two chromosomes which are involved in bridge formation at the divisional plane in Fig. 23 is evidence in favour of this assumption (cf. Table IV). In Fig. 25 two univalents are figured of which one is splitting (u) and the other has divided and is moving to the opposite pole ($u^1_1$ and $u^1_2$). Occasionally chromosomes have been seen reaching poles earlier than the rest of the chromosomes (Figs. 21 and 22, u). These are presumably the univalents which failed in their orientation in the preceding metaphase and had remained near the poles; these chromosomes often show a split at this time (Fig. 21, u).

Anaphase in this species is usually characterised by the presence of chromatid bridges and fragments

(Fig. 23, f). A typical bridge is shown in Fig. 26 along with 2 univalents (one of which is divided, $u^1_1$ and $u^1_2$ and the other is eliminated, u) while 10 chromosomes are arriving at either pole. The presence of a fragment at anaphase without any bridge (Fig. 24, f) seems to indicate that the bridge has either been disjoined early or carried to one of the poles leaving the fragment between the separating groups of chromosomes, the former of these two suggestions is more likely since bridges have not been seen at second anaphase.

The frequency of bridges, fragments and laggards has been analysed in 460 pollen-mother-cells at anaphase and is recorded in Table III.

The distribution of chromosomes at second metaphase was often unequal as might be expected owing to the splitting and elimination of univalents.

### TABLE III.

Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at first anaphase in 460 pollen-mother-cells of S. lanciforme.

| No. of P.M.C. showing clean separation | No. of Chromatid Bridges | No. of Fragments | No. of Laggards Unsplit 1 | Unsplit 2 | Split 1 | Split 2 | No. of Eliminated Chromosomes | Frequency |
|---|---|---|---|---|---|---|---|---|
| 409 | - | - | - | - | - | - | - | 409 |
| - | 1 | - | 1 | - | - | - | - | 15 |
| - | 1 | - | - | - | - | - | - | 5 |
| - | 1 | 1 | - | - | - | - | - | 2 |
| - | 1 | 1 | 1 | - | - | - | - | 1 |
| - | - | 1 | - | - | - | - | - | 4 |
| - | - | 1 | - | - | 1 | - | - | 1 |
| - | 1 | 1 | - | - | - | - | 1 | 1 |
| - | 1 | - | 1 | - | 1 | - | - | 1 |
| - | 1 | - | - | - | 1 | - | 1 | 1 |
| - | - | - | 1 | - | - | - | - | 12 |
| - | - | - | - | - | 1 | - | - | 5 |
| - | - | - | - | - | - | 2 | - | 2 |
| - | - | - | - | - | - | - | 1 | 1 |
| Total P. M. C. analysed | | | | | | | | 460 |

The following distribution of chromosomes was noted at second metaphase plates:

### TABLE IV.

| Chromosome number on plates I | II | Eliminated Chromosomes | Frequency | Figure |
|---|---|---|---|---|
| 12 | 12 | - | 42 | 27 |
| 12 | 13 | - | 4 | 28 |
| 12 | 11 | 1 | 2 | 29 |
| Total P. M. C. analysed | | | 48 | |

The secondary associations have been observed to continue till the second metaphase when they were further studied. It is apparent from Table V and Figs 30-45 that although the most frequent combination was 4 groups of 2 and 4 single chromosomes as at the first metaphase, the types of associations were more numerous than at the first division (cf Table II). There are several instances in plants other than _Solanum_ where secondary association of chromosomes was more marked at second metaphase, e.g. in _Oryza_ (Nandi 1936), _Brassica_ (Sikka 1940).

TABLE V.

Showing character and frequency of secondary association in second metaphase in _S_. _lanciforme_.

| No. of single chromosomes | No. of chromosomes in groups of | | | Frequency | Figure |
|---|---|---|---|---|---|
| | 2 | 3 | 4 | | |
| 12 | - | - | - | 3 | 30 |
| 10 | 1 | - | - | 5 | 31 |
| 9 | - | 1 | - | 2 | 32 |
| 8 | 2 | - | - | 5 | 33 |
| 8 | - | - | 1 | 1 | 34 |
| 7 | 1 | 1 | - | 5 | 35 |
| 6 | 3 | - | - | 7 | 36 |
| 6 | - | 2 | - | 2 | 37 |
| 6 | 1 | - | 1 | 2 | 38 |
| 5 | 2 | 1 | - | 6 | 39 |
| 4 | 4 | - | - | 11 | 40 |
| 4 | 1 | 2 | - | 1 | 41 |
| 4 | 2 | - | 1 | 1 | 42 |
| 3 | 3 | 1 | - | 2 | 43 |
| 2 | 3 | - | 1 | 2 | 44 |
| 1 | 4 | 1 | - | 1 | 45 |
| Total P.M.C. analysed | | | | 56 | |

Second anaphases are more regular than the first although this could not be analysed in a large number of pollen-mother-cells. Fig. 46 shows a second anaphase with an eliminated chromosome.

II. S. Parodii sp. coll. Juz. et Buk.

Twelve bivalents have been noted at diakinesis. A small chromatin body (Fig. 47, f, outlined) has often been observed together with 12 bivalents at this stage; judging from its size it can only be interpreted as a fragment, and its presence at metaphase (Fig. 52, f, and cf. Table VI) supports this assumption.

At metaphase as usual bivalents are orientated on the equatorial plate so that in polar view 12 bivalents are seen (Fig. 54). The occasional presence of 13 chromosomes on the plate must be considered as due to the presence of 11 bivalents and 2 univalents (Fig. 50 $u_1$ and $u_2$). In Fig. 50 the univalents (presumed from their peculiar shape) lie in close proximity, this suggests that they are secondarily associated (also Fig. 51 $u_{II}$). This secondary pairing among univalents is to be expected since they are homologous and could be recognised by the presence of all the chromosomes as bivalents in a large number of instances (cf. Table VI). Moffett (1931) in the triploid Pyrus minima recorded secondary pairing among univalents, which he regarded as being caused by their mutual attraction following from their homology though he considered that the homology was not sufficient for prophase pairing as evidenced by the high frequency of univalents.

TABLE VI.

Showing frequency of bivalents, univalents and fragments at first metaphase in 247 pollen-mother-cells of S. Parodii sp. coll. Juz. et Buk.

| Metaphase complement | Frequency | Figure |
|---|---|---|
| 12 bivalents | 237 | 48 |
| 11 bivalents and 2 univalents | 7 | 49 |
| 12 bivalents and 1 fragment | 3 | 52 |
| Total P.M.C. analysed | 247 | |

Side views of metaphase plates in this species are often characterised by non-congression of bivalents, these are either rod or ring type. Fig. 53 shows a non-orientated ring bivalent (in black) at metaphase.

Secondary associations between bivalents were quite marked in polar view of metaphase. Table VII shows the types of associations observed in 148 metaphase plates. The various types of associations have been illustrated in Figs. 55-73.

TABLE VII.

Showing character and frequency of secondary associations at first metaphase in S. Parodii.

| No. of single bivalents | No. of bivalents in groups of 2 | 3 | 4 | 5 | Frequency | Figure |
|---|---|---|---|---|---|---|
| 12 | - | - | - | - | 6 | 54 |
| 10 | 1 | - | - | - | 16 | 55 |
| 9 | - | 1 | - | - | 8 | 56 |
| 8 | 2 | - | - | - | 18 | 57 |
| 8 | - | - | 1 | - | 3 | 58 |
| 7 | 1 | 1 | - | - | 12 | 59 |
| 6 | 3 | - | - | - | 22 | 60 |
| 6 | 1 | - | 1 | - | 3 | 61 |
| 5 | 2 | 1 | - | - | 6 | 62 |
| 5 | 1 | - | - | 1 | 4 | 63 |
| 5 | - | 1 | 1 | - | 3 | 64 |
| 4 | 4 | - | - | - | 29 | 65 |
| 4 | 1 | 2 | - | - | 4 | 66 |
| 4 | 2 | - | 1 | - | 1 | 67 |
| 3 | 3 | 1 | - | - | 6 | 68 |
| 3 | 1 | 1 | 1 | - | 1 | 69 |
| 3 | 2 | - | - | 1 | 1 | 70 |
| 2 | 1 | 1 | - | 1 | 1 | 71 |
| 2 | 3 | - | 1 | - | 1 | 72 |
| 2 | 5 | - | - | - | 3 | 73 |
| Total P.M.C. analysed | | | | | 148 | |

At first anaphase the chromosomes of the paired bivalents are the first to disjoin to opposite poles leaving the univalents midway between them. The splitting of univalents was determined by their position on the spindle in relation to the equatorial plate. Those univalents which happened to lie near to or actually on the equator of the spindle seem to split (Fig. 75, and Table VIII) while other univalents which lie near the pole pass intact to their respective poles (Fig. 74, u). In the majority of cases at the completion of the division the univalents are included in the daughter nuclei, but a few of these occasionally lag and were found to lie off the plate at second division (Fig. 99).

Frequently a chromatid bridge and a fragment has been observed at first anaphase. The chromatid bridge is short and the fragment is fairly large (Fig. 76, f). At a later stage of anaphase the bridge breaks and the chromatids pass to the poles leaving the fragment on the divisional plane (Fig. 77, f).

### TABLE VIII.

Showing frequency of lagging chromosomes at first anaphase in 259 pollen-mother-cells of <u>S. Parodii</u>

| No. of P.M.C. showing clean separation | No. of Laggards | | No. of P.M.C. showing other irregularities | Frequency |
|---|---|---|---|---|
| | Unsplit | Split | | |
| 227 | - | - | - | 227 |
| - | 1 | - | - | 3 |
| - | - | 1 | - | 3 |
| - | - | - | 26 | 26 |
| Total P.M.C. analysed | | | | 259 |

TABLE IX.

Showing frequency of chromatid bridges and fragments at first anaphase in 259 pollen-mother-cells of S. Parodii.

| No. of P.M.C. showing clean separation | No. of chromatid bridges | | No. of Fragments | No. of P.M.C. showing other irregularities | Frequency |
|---|---|---|---|---|---|
| | 1 | 2 | | | |
| 227 | - | - | - | - | 227 |
| - | 1 | - | - | - | 20 |
| - | 1 | - | 1 | - | 1 |
| - | - | - | 1 | - | 5 |
| - | - | - | - | 6 | 6 |
| Total P.M.C. analysed | | | | | 259 |

Table IX shows that the fragments are hardly ever seen together with the bridges. This may be due either to their being concealed by the chromosomes forming the bridge or their having been carried to one of the poles by the separating chromosomes.

It is often noted at this time that bivalents which do not separate promptly lag behind the two separating groups of chromosomes. The configuration of such bivalents cannot be confused with the bridge separation since they behave in a different manner (cf. Figs. 76 and 78). Judging from the configuration (Fig. 78, in black) the bivalents separate with difficulty this may be due to the prevention of movement in the chiasmata. Instances of delayed separation of bivalents due to persistance of chiasmata are not rare, e.g. in Lachenalia (Moffett 1936a), Viola striata (Clausen 1929), Brassica oleracea (Richharia 1937). The view has been expressed that change in the homology of chromosomes may lead to difficulty in movement of the chiasmata towards the extremity (Darlington 1931, Erlanson 1931, Sansome 1932). If this be so, then the fragmentation of chromosomes regarded as due to the change in the homology of the chromosomes through segmental interchange (Philp and Huskins 1931), along with the phenomenon of difficulty in movement of chiasmata seem to suggest that some sort of segmental change, although short, has occurred in the chromosomes of S. Parodii.

Fig. 79 shows a polar view of anaphase; the separating groups have been shown more widely spaced out than they actually are in the pollen-mother-cell but the spatial relationship of the individual chromosomes has been maintained. In this figure the chromosome groups of one side (in black) correspond approximately with the other (dotted). This secondary association is to be expected if it is an inherent property of chromosomes themselves and is not merely a "clumping" due to fixation. This stage does not lend itself to the analysis of the secondary association and this aspect had to be passed over. In Pyrus arbutifolia, Moffett (1931) figured chromosomal grouping corresponding exactly at this stage as was to be expected.

At second metaphase the secondary association was conspicuous. Table X and Figs 81-97 show the different types of associations.

TABLE X.

Showing character and frequency of secondary associations at second metaphase in S. *Parodii*.

| No. of single chromosomes | No. of chromosomes in groups of | | | | Frequency | Figure |
|---|---|---|---|---|---|---|
| | 2 | 3 | 4 | 5 | | |
| 12 | - | - | - | - | 7 | 80 |
| 10 | 1 | - | - | - | 13 | 81 |
| 9 | - | 1 | - | - | 8 | 82 |
| 8 | 2 | - | - | - | 21 | 83 |
| 8 | - | - | 1 | - | 2 | 84 |
| 7 | 1 | 1 | - | - | 16 | 85 |
| 6 | 3 | - | - | - | 23 | 86 |
| 6 | 1 | - | 1 | - | 6 | 87 |
| 6 | - | 2 | - | - | 2 | 88 |
| 5 | 2 | 1 | - | - | 7 | 89 |
| 5 | 1 | - | - | 1 | 2 | 90 |
| 4 | 4 | - | - | - | 30 | 91 |
| 4 | 2 | - | 1 | - | 4 | 92 |
| 4 | 1 | 2 | - | - | 2 | 93 |
| 4 | - | 1 | - | 1 | 1 | 94 |
| 3 | 3 | 1 | - | - | 2 | 95 |
| 2 | 5 | - | - | - | 5 | 96 |
| 2 | 3 | - | 1 | - | 2 | 97 |
| Total P.M.C. analysed | | | | | 153 | |

Distribution of chromosomes on the second metaphase plates was, on the whole, regular (Fig. 98). Fig. 99a shows a distribution of 12-11 chromosomes, the 11-chromosome plate is cut, and the 11th chromosome was picked up in the next section (Fig. 99b). In this figure there is one chromosome and a fragment (f) lying off the plate.

Second anaphases are comparatively regular although occasionally lagging chromosomes are seen (Fig. 100, in black).

### III. S. infundebuliforme Phil.

#### (a) Cytomyxis:

Gates in 1911 proposed the term cytomyxis for a phenomenon he had observed in Oenothera. He applied the term to cases amongst pollen-mother-cells dividing normally, wherein certain cells at synezesis the nucleus approaches the cell wall and chromatin passes through from one cell to the other. Such cases have been observed in these studies in S. infundibuliforme at early (Fig. 2) and late stages of division (Fig. 2a). Two explanations have been offered on cytomyxis. On the one hand, many authorities regard it as merely a fixation artifact. Gates himself, however, followed by Gates and Rees (1921) in Lactuca and Church (1929) in Panicum have shown its regular occurrence. Sakamura (1916) working with Vicia faba showed that the incidence of cytomyxis was greatly increased in anthers previously treated with chloral. Church in the 1929 paper expresses the opinion that the high degree of pollen-sterility found in Panicum and Festuca is largely due to the naturally occurring incidence of cytomyxis in species of these two genera. In the material reported on here from S. infundibuliforme there is no reason to suspect that the observed cytomyxis is a fixation product but rather that it is typical of the species and, insofar as it occurs, is natural. How far cytomyxetic cells provide sterile or "empty" pollen grains or how far they may be subsequently absorbed is difficult to determine.

### (b) Lack of synchronization in pollen-mother-cells:

The normal condition in an anther is for all the pollen-mother-cells to proceed to meiosis simultaneously but in S. infundibuliforme this was not so. Anthers from this species showed cells at different stages and in fact many were found in very early prophase when the greater proportion were at metaphase of the first division (Fig. 3). The ultimate fate of these delayed cells was extremely difficult to follow, for when anthers in later stages were examined delayed cells were not found. Whether they are absorbed and so disappear or their late commencement is followed by an expediting of the processes which follow could not be decided.

Frankel (1940) working with Hebe Townsoni found male sterility was associated with this divisional mistiming in meiosis. Upcott (1937a) found that increased spiralization and terminalization occurred when mistiming was observed and these phenomena were precursors of male sterility.

In potato one would assume that timing idiosyncrasies are connected with genotypic control rather than that they are a reflex of the phenotypic condition.

The fact that irregular commencement of division was apparently cancelled, was clear in second division for here synchronization of the cells was normal.

(c) First and second division:

This species also shows 12 bivalents both at diakinesis (Fig. 101) and at metaphase (Fig. 106). The chromosomes are mostly held by terminal chiasmata at these stages, although bivalents showing non-terminalized chiasmata were not rare (Fig. 102, a and b).

Table XI shows the frequency of univalents and fragments which were seen at metaphase. The fragmentation of chromosomes at this stage (Fig. 104,f) recalls the instances of <u>S. Parodii</u> where similar fragments were noted (cf. page 13).

TABLE XI.

Showing chromosome complements at first metaphase in 255 pollen-mother-cells of <u>S. infundibuliforme.</u>

| Chromosome complement | Frequency | Figure |
|---|---|---|
| 12 bivalents | 232 | 102 |
| 11 bivalents and 2 univalents | 7 | 103 |
| 12 bivalents and 1 fragment | 16 | 104 |
| Total P.M.C. analysed | 255 | |

Non-orientation of bivalents are often seen at metaphase, an instance of which is shown in Fig. 105. In this figure the bivalent in question (in black) shows an interstitial chiasma.

Here again the bivalents show secondary association the frequency of which is tabulated in Table XII and illustrated in Figs. 107-118.

TABLE XII.

Showing character and frequency of secondary associations at first metaphase in <u>S. infundibuliforme</u>.

| No. of single bivalents | No. of bivalents in groups of 2 | 3 | 4 | 5 | Frequency | Figure |
|---|---|---|---|---|---|---|
| 12 | - | - | - | - | 10 | 106 |
| 10 | 1 | - | - | - | 11 | 107 |
| 9 | - | 1 | - | - | 12 | 108 |
| 8 | 2 | - | - | - | 11 | 109 |
| 8 | - | - | 1 | - | 4 | 110 |
| 7 | 1 | 1 | - | - | 8 | 111 |
| 7 | - | - | - | 1 | 2 | 112 |
| 6 | 3 | - | - | - | 11 | 113 |
| 6 | 1 | - | 1 | - | 2 | 114 |
| 6 | - | 2 | - | - | 1 | 115 |
| 5 | 2 | 1 | - | - | 2 | 116 |
| 4 | 4 | - | - | - | 15 | 117 |
| 4 | - | 1 | - | 1 | 1 | 118 |
| Total P.M.C. analysed | | | | | 90 | |

Pollen-mother-cells with the unreduced number of 24 chromosomes were observed at metaphases. In Fig. 119 in addition to the 24 chromosomes there is a small chromatin body (S), presumably a satellite. The nature of this body could not be confirmed as somatic chromosomes were not studied. Since Rosenberg (1909) first recorded restitution nuclei with 2n chromosomes, it has been frequently recorded in hybrids and polyploids. These diploid cells may arise owing to irregularity during first division, i.e. failure of chromosomes to orientate on the metaphase plate, e.g. triploid Tulipa, Newton and Darlington (1929) or through failure of an archesporial nucleus to complete division after splitting of the chromosomes (Karpechenko 1927).

At first anaphase the univalents lag (Fig. 122, and Table XIII) while bivalents disjoin.

TABLE XIII

Showing frequency of fragments, lagging and eliminated chromosomes at first metaphase in 136 pollen-mother-cells of S. infundibuliforme.

| No. of P.M.C. showing clean separation | No. of Fragments | No. of Laggards |  | Eliminated chromosomes | Frequency |
|---|---|---|---|---|---|
|  |  | Unsplit | Split |  |  |
| 122 | - | - | - | - | 122 |
| - | 1 | - | - | - | 5 |
| - | 1 | 1 | - | - | 2 |
| - | - | 1 | - | - | 4 |
| - | - | - | 1 | - | 2 |
| - | - | - | - | 2 | 1 |
| Total P.M.C. analysed |  |  |  |  | 136 |

Fig. 120 shows a distribution of 11 and 12 chromosomes while a divided univalent is lagging between two separated chromosome groups. In one pollen-mother-cell at this stage two chromosomes have been seen lying off the spindle (Fig. 121, in black), this presumably was a bivalent which failed to orientate at metaphase, and the chromosomes have separated late. The separation of 11 chromosomes at either pole in the figure justifies this assumption. In Fig. 123 equal distribution of 12 chromosomes has been figured and the chromosomes here have been drawn widely spaced out.

In Table XIV and Figs. 125-142 have been shown different types of secondary association observed at second metaphase.

TABLE XIV.

Showing character and frequency of secondary associations at second metaphase in S. *infundibuliforme*.

| No. of single chromosomes | No. of chromosomes in groups of | | | | Frequency | Figure |
|---|---|---|---|---|---|---|
| | 2 | 3 | 4 | 5 | | |
| 12 | - | - | - | - | 4 | 124 |
| 10 | 1 | - | - | - | 6 | 125 |
| 9 | - | 1 | - | - | 2 | 126 |
| 8 | 2 | - | - | - | 14 | 127 |
| 8 | - | - | 1 | - | 1 | 128 |
| 7 | 1 | 1 | - | - | 10 | 129 |
| 7 | - | - | - | 1 | 1 | 130 |
| 6 | 3 | - | - | - | 12 | 131 |
| 6 | 1 | - | 1 | - | 3 | 132 |
| 6 | - | 2 | - | - | 2 | 133 |
| 5 | 2 | 1 | - | - | 4 | 134 |
| 5 | 1 | - | - | 1 | 2 | 135 |
| 4 | 4 | - | - | - | 17 | 136 |
| 4 | 1 | 2 | - | - | 3 | 137 |
| 4 | 2 | - | 1 | - | 3 | 138 |
| 3 | 1 | 1 | 1 | - | 2 | 139 |
| 3 | 2 | - | - | 1 | 2 | 140 |
| 3 | 3 | 1 | - | - | 1 | 141 |
| 2 | 5 | - | - | - | 4 | 142 |
| Total P.M.C. analysed | | | | | 93 | |

Second anaphase is more irregular (Fig. 143 $u^1_1$, $u^1_2$ and el) than the first (cf Table XIII and XV). The univalents lag and divide or are eliminated (el) at this time. In Fig. 144 as many as three eliminated chromosomes (el) and a lagging chromosome which has divided ($u^1_1$ and $u^1_2$) have been shown. In this figure a small fragment (f) is also shown.

Chromatid bridges have been observed at this time (Fig. 145) although they are rare (cf Table XV). The absence of such bridges in the first division seems to indicate that the chromosomes forming them in second division pass to the poles undisjoined and separate only at the second division. The presence of fragments in between the separating groups of chromosomes at anaphase without any chromatid bridges suggests that it is a possibility.

Occasionally pollen-mother-cells have been seen at second anaphase where the chromosomes are scattered on the spindle as if they had failed in their orientation on the spindle plate, at the preceding stage, i.e. second metaphase. An extreme instance of this sort of thing is represented in Fig. 146; here two chromatid bridges are seen (in black) at either side together with 22 chromosomes on each spindle. Darlington and Thomas (1937) in <u>Festuca</u>-<u>Lolium</u>

derivatives demonstrated similar scattering of chromosomes at first metaphase as a result of "incompact spindle" and studied the consequence of such spindles on cell divisions during meiosis.

TABLE XV.

Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at second metaphase in 103 pollen-mother-cells of <u>S. infundibuliforme</u>.

| No. of P.M.C. showing clean separation | No. of chromatid bridges | | No. of Fragments | No. of Laggards | | | | Eliminated chromosomes. | Frequency |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Unsplit | | Split | | | |
| | I | II | | I | II | I | II | | |
| 85 | - | - | - | - | - | - | - | - | 85 |
| - | 1 | - | - | - | - | - | - | - | 1 |
| - | 1 | 1 | - | - | - | - | - | - | 1 |
| - | - | - | 1 | - | - | - | - | - | 2 |
| - | - | - | 1 | - | - | 1 | - | 3 | 1 |
| - | - | - | - | 1 | - | - | - | - | 3 |
| - | - | - | - | - | - | 1 | - | 1 | 1 |
| - | - | - | - | - | - | - | - | 3 | 1 |
| - | - | - | - | - | - | - | - | 2 | 3 |
| - | - | - | - | - | - | - | - | 1 | 5 |
| Total P.M.C. analysed | | | | | | | | | 103 |

IV. S. stenotomum var. sp. coll. Juz. et Buk.

Twelve bivalents at diakinesis are seen to be scattered in the nucleus almost equidistant from each other. The smaller chromosomes are generally held by one terminal chiasma while the larger chromosomes are aften held together by chiasmata at both ends (Fig. 147).

Figure 152 is a polar view of first metaphase showing 12 bivalents. The number of bivalents is somewhat variable for complete pairing of all the chromosomes does not always occur. Fig. 149 is a side view of metaphase showing 11 bivalents and 2 univalents (u). It is rather surprising to find in one instance a trivalent at metaphase. This chromosome complement is figured (Fig. 150) to show 1 trivalent, 10 bivalents and 1 univalent (u). The presence of a trivalent is important for it demands one of two possible explanations. On the one hand it may simply indicate an abnormal structure in invididual chromosomes while on the other hand it may indicate the presence of two homologues. This second explanation seems the more reasonable but it implies that this "diploid" species can no longer be accepted as diploid with a basic number of 12 chromosomes but rather a polyploid with a basic number of 6. This suggestion is in harmony with that of Lawrence (1931b) and Müntzing (1933) (cf. pp. 55-62).

The metaphase complement in 455 pollen-mother-cells was analysed, with the results shown in Table XVI.

TABLE XVI.

Chromosome complement at first metaphase in 455 pollen-mother-cells of S. stenotomum var.

| Metaphase complement | Frequency | Figure |
|---|---|---|
| 12 bivalents | 414 | 148 |
| 11 bivalents and 2 univalents | 40 | 149 and 151 (polar view) |
| 1 trivalent, 10 bivalents and 1 univalent | 1 | 150 |
| Total P.M.C. analysed | 455 | |

The secondary association between bivalents at metaphase is shown in the Table XVII and Figs. 153-168.

Fig. 169 shows non-congression of a bivalent at metaphase, a feature often noted in this species at this time.

At early anaphase bivalents with interstitial chiasmata seem to disjoin with difficulty and fail to move with the rest of their fellows. Lawrence (1931a) studying Dahlia hybrids noted the occurrence of interstitial chiasma in bivalents and ascribed the failure of terminalization to the linear differentiation of pairing chromosomes. In other words, the formation of an interstitial chiasma is an evidence of hybridity according to this author. The delayed separation of bivalents with interstitial chiasmata suggests that some sort of change has occurred in the chromosomes of S. stenotomum (cf. pp. 17-18).

TABLE XVII

Showing character and frequency of secondary associations at first metaphase in S. stenotomum var.

| No. of single bivalents | No. of bivalents in groups of 2 | 3 | 4 | 5 | Frequency | Figure |
|---|---|---|---|---|---|---|
| 12 | - | - | - | - | 3 | 152 |
| 10 | 1 | - | - | - | 3 | 153 |
| 9 | - | 1 | - | - | 1 | 154 |
| 7 | 1 | 1 | - | - | 1 | 155 |
| 6 | 3 | - | - | - | 6 | 156 |
| 6 | 1 | - | 1 | - | 2 | 157 |
| 5 | 2 | 1 | - | - | 4 | 158 |
| 5 | - | 1 | 1 | - | 1 | 159 |
| 4 | 4 | - | - | - | 8 | 160 |
| 4 | 2 | - | 1 | - | 4 | 161 |
| 4 | 1 | 2 | - | - | 2 | 162 |
| 3 | 3 | 1 | - | - | 6 | 163 |
| 3 | 1 | 1 | 1 | - | 1 | 164 |
| 3 | 2 | - | - | 1 | 2 | 165 |
| 2 | 5 | - | - | - | 2 | 166 |
| 2 | 3 | - | 1 | - | 2 | 167 |
| 1 | 1 | 3 | - | - | 1 | 168 |
| Total P.M.C. analysed | | | | | 49 | |

The univalents at anaphase split or divide while lagging (Figs. 175 $u^1{}_1$ and $u^1{}_2$; 176 $u^1{}_1$, $u^1{}_2$ and u) or are carried to the poles undivided.

Division of univalents lagging on the divisional plane has very often been reported in other plants and hybrids. In pentaploid wheat hybrids all the seven univalents always divide during the first division (Kihara 1924). Clausen (1926) refers to division of univalents in Viola hybrids at anaphase, especially in *Viola arvensis* x *V. maritima* where the number of univalents is high. The latter author attached special importance to the phenomenon and regarded it as a means of increase in chromosome number in species of hybrid origin. The situation is similar in *Phleum* hybrids (Müntzing 1935) though the number of dividing univalents is variable as in the *Solanum* species. The frequency of lagging univalents has been analysed in 219 pollen-mother-cells (Table XVIII).

In Table XIX is shown the frequency of bridges and fragments which are commonly seen at anaphase. Fig 172 shows a typical long bridge with a small fragment (f) and is to be compared with Figs. 171 and 173 where a small bridge and a large fragment is shown. The fragment (f) in Fig. 173 is splitting. The size of the fragment is inversely proportional to the length of the bridge and the length of the bridge depends on the position of the inverted segment relative to the centromere, if close to it is short, and if relatively distant it is long. Hence the size of the fragments may be taken as a measure for judging the position of an inverted segment (Darlington 1937). Sax (1937) in Paeonia suffruticosa however, considered that cross-overs in non-homologously paired chromosomes is the cause of variation in fragment size.

TABLE XVIII.

Showing frequency of lagging chromosomes and early reaching of univalents at poles at first metaphase in 219 pollen-mother-cells of S. stenotomum var.

| No. of P.M.C. showing clean separation | No. of Laggards Unsplit 1 | | Split 1 | 2 | No. of chromosomes reaching poles early | No. of P.M.C. showing other irregularities | Frequency |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | | | | | |
| 176 | - | - | - | - | - | - | 176 |
| - | 1 | - | - | - | - | - | 2 |
| - | - | - | 1 | - | - | - | 8 |
| - | - | - | - | 2 | - | - | 1 |
| - | 1 | - | - | - | 1 | - | 2 |
| - | - | - | 1 | - | 1 | - | 2 |
| - | - | - | - | - | - | 28 | 28 |
| Total P.M.C. analysed | | | | | | | 219 |

TABLE XIX.

Showing frequency of chromatid bridges and fragments at first anaphase in 219 pollen-mother-cells of S. stenotomum var.

| No. of P.M.C. showing clean separation | No. of chromatid bridges | No. of Fragments 1 | 2 | No. of P.M.C. showing other irregularities | Frequency |
|---|---|---|---|---|---|
| 176 | - | - | - | - | 176 |
| - | 1 | 1 | - | - | 17 |
| - | 1 | - | - | - | 6 |
| - | 1 | - | 2 | - | 2 |
| - | - | 1 | - | - | 3 |
| - | - | - | - | 15 | 15 |
| Total P.M.C. analysed | | | | | 219 |

First division is succeeded by a resting period. The interphase nuclei often differ in size amongst themselves owing, it is thought, to the varying number of chromosomes which they contain. The eliminated chromosomes which form micro-nuclei are generally small and are formed around univalents (Fig. 177) or half univalents.

Secondary associations of various types have been observed at second metaphase (Table XX), and figured in Figs. 179-193.

TABLE XX.

Showing character and frequency of secondary associations at second metaphase in S. stenotomum var.

| No. of single chromosomes | No. of chromosomes in groups of 2 | 3 | 4 | 5 | Frequency | Figure |
|---|---|---|---|---|---|---|
| 12 | - | - | - | - | 5 | 178 |
| 10 | 1 | - | - | - | 6 | 179 |
| 9 | - | 1 | - | - | 2 | 180 |
| 8 | 2 | - | - | - | 7 | 181 |
| 8 | - | - | 1 | - | 1 | 182 |
| 7 | 1 | 1 | - | - | 4 | 183 |
| 6 | 3 | - | - | - | 17 | 184 |
| 6 | 1 | - | 1 | - | 1 | 185 |
| 5 | 2 | 1 | - | - | 2 | 186 |
| 4 | 4 | - | - | - | 24 | 187 |
| 4 | 1 | 2 | - | - | 1 | 188 |
| 3 | 3 | 1 | - | - | 2 | 189 |
| 2 | 5 | - | - | - | 3 | 190 |
| 2 | 2 | 2 | - | - | 2 | 191 |
| 2 | 3 | - | 1 | - | 3 | 192 |
| 1 | 4 | 1 | - | - | 1 | 193 |
| Total P.M.C. analysed | | | | | 81 | |

The distribution of chromosomes was unequal as might be expected owing to the splitting, and random separation of univalents. The following distribution of chromosomes was noted on the plates:-

TABLE XXI.

Showing chromosome distribution on second metaphase plates in S. stenotomum var.

| No. of chromosomes on metaphase plates I | II | Frequency | Figure |
|---|---|---|---|
| 12 | 12 | 51 | 194 |
| 12 | 13 | 3 | 195 |
| 13 | 13 | 2 | 196 |
| 12 | 14 | 1 | 197 |
| 11 | 15 | 3 | 198 |
| Total P.M.C. analysed | | 60 | |

The unusually high chromosome number on the second metaphase plates figured (Figs. 198a; 197a; 195a) shows without doubt that the univalents have divided before being included in the plates. Federley (1913) observed in Pygaera hybrids that the univalent chromosomes divide in the first metaphase, and as a consequence the number of chromosomes on the second division is increased, sometimes to such an extent that the number of chromosomes is double the expected number. In Viola hybrids (Clausen 1926), and Limonium binervosum, broad-leaved form which is a spontaneous hybrid (Choudhuri 1942), increase in chromosome number takes place by division of univalents at anaphase.

Second anaphase is almost as irregular as the first (Table XXII). The spindles are generally parallel or at right angles to the plane of first division. Not infrequently lagging chromosomes have been seen at this time (Fig. 199). Fig. 200 shows a lagging univalent which is dividing and one eliminated chromosome which is presumably an half univalent. The distribution of 11-12 (dotted) and 11-11 (outlined) is in favour of such an assumption.

TABLE XXII.

Showing frequency of chromatid bridges, fragments, lagging and eliminated chromosomes at second anaphase in 94 pollen-mother-cells of *S. stenotomum* var.

| No. of P.M.C. showing clean separation | No. of bridges | No. of fragments | No. of laggards Unsplit I | | split I | II | No. of eliminated chromosomes | Frequency |
|---|---|---|---|---|---|---|---|---|
| | | | I | II | I | II | | |
| 72 | - | - | - | - | - | - | - | 72 |
| - | 1 | - | - | - | - | - | - | 9 |
| - | 1 | 1 | - | - | - | - | - | 4 |
| - | - | 1 | - | - | 1 | - | - | 1 |
| - | - | - | 1 | - | - | - | - | 3 |
| - | - | - | - | - | 1 | - | - | 1 |
| - | - | - | 1 | 1 | - | - | - | 1 |
| - | - | - | - | - | 1 | - | 1 | 1 |
| - | - | 1 | - | - | 1 | - | 1 | 1 |
| - | - | - | - | - | - | - | 1 | 1 |
| Total P.M.C. analysed | | | | | | | | 94 |

Frequently chromatid bridges were observed at second anaphase (Table XXII). In Fig. 201 a pollen-mother-cell is figured to show a typical bridge together with a fragment (f) which had been freed during first anaphase.

V. S. Rybinii, Juz. et Buk.

In this species it has been possible to follow mid-diplotene where 12 bivalents were identified. In Fig. 202 bivalents are shown more widely spaced than in the actual nucleus. The chromosomes are generally held by terminal chiasmata although two bivalents (a and b) show that their chromosomes are held by interstitial chiasmata.

At diakinesis, the bivalents are more contracted and are evenly spaced in the nucleus (Fig. 203).

Table XXIII shows the chromosome complement at metaphase, where occasionally one bivalent is represented by two univalents.

TABLE XXIII.

Chromosome complement in 342 pollen-mother-cells of S. Rybinii.

| Metaphase complement | Frequency | Figure |
|---|---|---|
| 12 bivalents | 333 | 204 |
| 11 bivalents and 2 univalents | 9 | 205 |
| Total P.M.C. analysed | 342 | |

Secondary associations have been analysed in 79 first metaphase plates (Table XXIV). Various types of associations are shown in Figs. 207-223.

Few first anaphases have been seen, so complete observation was not possible at this stage, although a pollen-mother-cell was seen which showed two chromatid bridges together with three fragments (Fig. 225,f). The presence of a third fragment (outlined in the figure), however, suggests that fragments are formed in this species in some other way than by the bridge formation and this fragment has been traced back to a point as early as metaphase (Fig. 224, f).

TABLE XXIV.

Showing character and frequency of secondary associations at first metaphase in S. Rybinii.

| No. of single bivalents | No. of bivalents in groups of | | | | Frequency | Figure |
|---|---|---|---|---|---|---|
| | 2 | 3 | 4 | 5 | | |
| 12 | - | - | - | - | 5 | 206 |
| 10 | 1 | - | - | - | 6 | 207 |
| 9 | - | 1 | - | - | 4 | 208 |
| 8 | 2 | - | - | - | 8 | 209 |
| 8 | - | - | 1 | - | 3 | 210 |
| 7 | 1 | 1 | - | - | 4 | 211 |
| 7 | - | - | - | 1 | 1 | 212 |
| 6 | 3 | - | - | - | 15 | 213 |
| 6 | 1 | - | 1 | - | 2 | 214 |
| 5 | 2 | 1 | - | - | 5 | 215 |
| 4 | 4 | - | - | - | 18 | 216 |
| 4 | 2 | - | 1 | - | 2 | 217 |
| 4 | 1 | 2 | - | - | 1 | 218 |
| 3 | 3 | 1 | - | - | 1 | 219 |
| 3 | 1 | 1 | 1 | - | 1 | 220 |
| 2 | 3 | - | 1 | - | 1 | 221 |
| 2 | 2 | 2 | - | - | 1 | 222 |
| - | 3 | 2 | - | - | 1 | 223 |
| Total P.M.C. analysed | | | | | 79 | |

Owing to lack of material, complete observation on the second division could not be made.

VI. S. polyadenium, Greenman.

Diakinesis in this species shows 12 bivalents (Fig. 226), these are well spaced and mostly of the ring type, having one terminal chiasma at each end.

Fig. 229 is a polar view of first metaphase showing 12 bivalents, while Fig. 228 illustrates 11 bivalents and 2 univalents (u) at a side view. Often fewer than 2 univalents have been observed without any corresponding increase of paired chromosomes. The univalents may be at the same level as the bivalents at metaphase and are then obscured by bivalents. This is undoubtedly the reason why only one univalent appears in some nuclei. The frequency of univalents at this time has been analysed in 353 pollen-mother-cells (Table XXV).

TABLE XXV.

Showing frequency of univalents at first metaphase in 353 pollen-mother-cells of S. polyadenium.

| Chromosome complement | Frequency | Figure |
|---|---|---|
| 12 bivalents | 343 | 227 |
| 11 bivalents and 2 univalents | 10 | 228 |
| Total P.M.C. analysed | 353 | |

Various types of secondary associations noted at first metaphase are shown in Table XXVI and Figs.

230-244.

TABLE XXVI.

Showing character and frequency of secondary associations at first metaphase in *S. polyadenium*.

| No. of single bivalents | No. of bivalents in groups of | | | | Frequency | Figure |
|---|---|---|---|---|---|---|
| | 2 | 3 | 4 | 5 | | |
| 12 | - | - | - | - | 8 | 229 |
| 10 | 1 | - | - | - | 10 | 230 |
| 9 | - | 1 | - | - | 4 | 231 |
| 8 | 2 | - | - | - | 5 | 232 |
| 6 | 3 | - | - | - | 11 | 233 |
| 6 | 1 | - | 1 | - | 3 | 234 |
| 5 | 2 | 1 | - | - | 4 | 235 |
| 5 | 1 | - | - | 1 | 1 | 236 |
| 4 | 4 | - | - | - | 13 | 237 |
| 4 | 2 | - | 1 | - | 3 | 238 |
| 4 | 1 | 2 | - | - | 2 | 239 |
| 3 | 3 | 1 | - | - | 1 | 240 |
| 3 | 2 | - | - | 1 | 1 | 241 |
| 2 | 3 | - | 1 | - | 2 | 242 |
| 2 | 1 | 1 | - | 1 | 1 | 243 |
| 1 | 2 | 1 | 1 | - | 1 | 244 |
| Total P.M.C. analysed | | | | | 70 | |

At early anaphase small chromosomes with terminal chiasmata separate early whereas long chromosomes, and chromosomes with interstitial chiasma are delayed in separation. Such chromosomes are seen at this time with their two chromatids separated at the extremity (Fig. 245, in black).

Late anaphase is quite conspicuous by reason of the presence of chromatid bridges and fragments (Table XXVII). Fig. 246 shows a chromatid bridge and a fragment (f). In some instances two chromatid bridges have been noted as shown in figure 247. The presence of broken bridges and fragments without chromatid bridges (Fig. 249, f) was not rare. In Fig. 248 two fragments ($f_1$ and $f_2$) together with chromosomes whose chromatids are highly drawn out are figured (in black); these chromosomes probably had contributed to the formation of the bridge and this had subsequently broken. In this figure a univalent, near one of the poles, is also shown (u). The distribution of 12-11 chromosomes suggest that the other univalent is included in the 12-chromosome group.

TABLE XXVII.

Showing frequency of chromatid bridges and fragments at first anaphase in 349 pollen-mother-cells of S. polyadenium.

| No. of P.M.C. showing clean separation | No. of chromatid bridges | | No. of frag-ments | | No. of P.M.C. showing other irregularities | Frequency |
|---|---|---|---|---|---|---|
| | 1 | 2 | 1 | 2 | | |
| 286 | - | - | - | - | - | 286 |
| - | 1 | - | - | - | - | 23 |
| - | 1 | - | 1 | - | - | 3 |
| - | - | 2 | - | - | - | 6 |
| - | - | - | 1 | - | - | 18 |
| - | - | - | - | 2 | - | 1 |
| - | - | - | - | - | 12 | 12 |
| Total P.M.C. analysed | | | | | | 349 |

The univalents split while lagging on the divisional plane (Fig. 249). The frequency of lagging univalents has been tabulated in the Table XXVIII.

## TABLE XXVIII.

Showing frequency of lagging chromosomes at first anaphase in 349 pollen-mother-cells of S. polyadenium.

| No. of P.M.C. showing clean separation | No. of laggards Unsplit 1 | 2 | Split 1 | 2 | No. of P.M.C. showing other irregularities | Frequency |
|---|---|---|---|---|---|---|
| 286 | - | - | - | - | - | 286 |
| - | 1 | - | - | - | - | 5 |
| - | - | - | 1 | - | - | 6 |
| - | - | - | - | 2 | - | 1 |
| - | - | - | - | - | 51 | 51 |
| Total P.M.C. analysed | | | | | | 349 |

Here again, complete observation on the second division could not be made owing to the paucity of material.

## 5. MEIOSIS IN HYBRIDS.

### I. S. Parodii sp. coll. Juz. et Buk. x S. infundibuliforme Phil.

Early stages of the meiotic division could not be studied owing to difficulties of fixation, a problem which has been associated with hybridity by other investigators, and it has been already noted (cf. p. 6) that fixation of these stages is poor in certain of the recognised Solanum species.

Meiosis in the hybrid S. Parodii x infundibuliforme is broadly similar in many respects to that observed in hybrids generally. The parents of this hybrid have 12 chromosomes in their haploid nuclei. The similarity of chromosome number in the parents afforded no opportunity to study the mode of syndesis. The breeding results obtained from this cross (unpublished), however, indicate that pairing on the whole is allosyndetic, generally resulting in 12 bivalents. There can hardly be doubt that the 12 _Parodii_ chromosomes pair with all the _infundibuliforme_ chromosomes. The number of bivalents is not constant in all the nuclei; where there are less than 12 there is present a corresponding number of univalents (cf. Table XXIX).

Twelve bivalents could be made out at diakinesis, where the chromosomes often show interstitial chiasma (Fig. 250a).

In 189 pollen-mother-cells, the metaphase complement was analysed. The following metaphase complex was found:-

TABLE XXIX.

Showing chromosome complement in 189 pollen-mother-cells of _S. Parodii_ x _infundibuliforme_.

| Metaphase complement | Frequency | Figure |
|---|---|---|
| 12 bivalents | 179 | 253 |
| 11 bivalents and 2 univalents | 10 | 254 |
| Total P.M.C. analysed | 189 | |

In Fig. 254 the metaphase chromosomes from a pollen-mother-cell are shown; there are 11 bivalents and 2 univalents. The 2 univalents are lying off the equatorial plane and are split. Such precocious splitting of univalents has so far only been recorded in a few instances, e.g. in tetraploid spermatocytes of *Culex* (Moffett 1936b) and in pollen-mother-cells of *Limonium binervosum* (Choudhuri 1942).

Occasionally bivalents have been noted which have failed to become orientated on the equatorial region while the rest of the bivalents are arranged on the equatorial plate (Fig. 255). Church (1929) has demonstrated lagging and extrusion of bivalents at first metaphase division in *Paspalum muhlenbergii*, and in several species of *Panicum*. He correlated such abnormalities with established or suspected hybridity.

TABLE XXX.

Showing frequency of lagging chromosomes at first anaphase in 60 pollen-mother-cells of *S. Parodii* x *infundibuliforme*.

| No. of P.M.C. showing clean separation | No.of laggards Unsplit 1 | 2 | Split 1 | 2 | No. of P.M.C. showing other irregularities | Frequency |
|---|---|---|---|---|---|---|
| 55 | - | - | - | - | - | 55 |
| - | 1 | - | - | - | - | 2 |
| - | - | - | 1 | - | - | 1 |
| - | - | - | - | 2 | - | 1 |
| - | - | - | - | - | 1 | 1 |
| Total P.M.C. analysed | | | | | | 60 |

At first anaphase the bivalents separate normally, leaving the univalents in the equatorial region. The univalents split and behave in the same way as was shown by Müntzing (1935) in Phleum and in pentaploid wheat hybrids by Kihara (1924). In Table XXX is shown the frequency of lagging univalents at first anaphase. Fig. 256 shows lagging of two univalent chromosomes which are split: unequal distribution was often seen at this time. Fig. 257 shows separation of 11-12 together with a dividing univalent at the equatorial region. The unequal distribution in the figure shows that one univalent has been included in the 12-chromosome pole.

A chromatid bridge was seen in one instance although this feature could not be analysed in a large number of cells (Table XXXI). In Fig. 258 is shown a chromatid bridge. In this figure there are 12-11 chromosomes at poles, this is presumably due to the inclusion of one split univalent at one pole and one undivided univalent at the other. At late anaphase the bridge breaks (Fig. 259).

TABLE XXXI.

Showing frequency of chromatid bridges and fragments at first anaphase in 60 pollen-mother-cells of S. Parodii x infundibuliforme.

| No. of P.M.C. showing clean separation | No. of chromatid bridges | No. of fragments | No. of P.M.C. showing other irregularities | Frequency |
|---|---|---|---|---|
| 55 | - | - | - | 55 |
| - | 1 | - | - | 1 |
| - | - | - | ~~5~~4 | ~~5~~4 |
| Total P.M.C. analysed | | | | 60 |

Fig 160 shows a polar view of first anaphase with 12 chromosomes at each end, the chromosomes here are drawn widely spaced.

In this hybrid the first and second divisions are separated by a resting period. The interphase nuclei often show an unequal number of chromosomes. In Fig. 261 is figured a pollen-mother-cell which shows 12 and 13 chromosomes in its two nuclei; in the figure two chromosomes in the 13-chromosome nuclei (a and b) show wide separation of sister chromosomes which are held together only in the attachment region.

Table XXXII and Figs 263-284 show the different types of secondary associations seen at second metaphase, which was also seen at first metaphase (Figs 251 and 252) but could not be analysed in a sufficiently large number of cells since few polar views were obtained.

TABLE XXXII.

Showing character and frequency of secondary associations at second metaphase in S. *Parodii* x *infundibuliforme*.

| No. of single chromosomes | No. of chromosomes in groups of | | | | | Frequency | Figure |
|---|---|---|---|---|---|---|---|
| | 2 | 3 | 4 | 5 | 6 | | |
| 12 | - | - | - | - | - | 4 | 262 |
| 10 | 1 | - | - | - | - | 3 | 263 |
| 9 | - | 1 | - | - | - | 3 | 264 |
| 8 | 2 | - | - | - | - | 9 | 265 |
| 8 | - | - | 1 | - | - | 2 | 266 |
| 7 | 1 | 1 | - | - | - | 3 | 267 |
| 7 | - | - | - | 1 | - | 1 | 268 |
| 6 | 3 | - | - | - | - | 12 | 269 |
| 6 | - | 2 | - | - | - | 3 | 270 |
| 6 | 1 | - | 1 | - | - | 2 | 271 |
| 5 | 2 | 1 | - | - | - | 4 | 272 |
| 5 | 1 | - | - | 1 | - | 2 | 273 |
| 4 | 4 | - | - | - | - | 19 | 274 |
| 4 | 1 | 2 | - | - | - | 2 | 275 |
| 4 | 2 | - | 1 | - | - | 2 | 276 |
| 4 | - | 1 | - | 1 | - | 1 | 277 |
| 3 | 3 | 1 | - | - | - | 6 | 278 |
| 3 | 2 | - | - | 1 | - | 1 | 279 |
| 3 | 1 | 1 | 1 | - | - | 1 | 280 |
| 3 | - | 1 | - | - | 1 | 2 | 281 |
| 2 | 5 | - | - | - | - | 3 | 282 |
| 2 | 3 | - | 1 | - | - | 1 | 283 |
| 1 | 2 | 1 | 1 | - | - | 2 | 284 |
| Total P.M.C. analysed | | | | | | 88 | |

The distribution of chromosomes on the second metaphase plate was occasionally unequal as might be expected owing to splitting of univalents (Table XXXIII). In Fig. 285 one chromosome at either plate is highly elongated; it is very probable that these two chromosomes were involved in bridge formation during first division and therefore separated late.

TABLE XXXIII.

Showing distribution of chromosomes on second metaphase plates in *S. Parodii* x *infundibuliforme*.

| No. of chromosomes on plates I | II | Frequency | Figure |
|---|---|---|---|
| 12 | 12 | 67 | 286 |
| 12 | 13(a) | 3 | 287 |
| Total P.M.C. analysed | | 70 | |

Second anaphases often showed irregularities (Table XXXIV). In Fig. 288 one lagging univalent is figured (which is split) together with the distribution of 12-12 (dotted) and 11-11 chromosomes (outlined), whereas Fig. 289 shows one lagging chromosome at either side. In this figure the distribution of chromosomes is 11-11 and 11-12; this shows that the lagging chromosome ($u^1$) is an half univalent and the other half has been included in the 12-chromosome group.

TABLE XXXIV.

Showing frequency of lagging chromosomes at second anaphase in 57 pollen-mother-cells of *S. Parodii* x *infundibuliforme.*

| No. of P.M.C. showing clean separation | No. of laggards I | II | I | II | Frequency |
|---|---|---|---|---|---|
| 49 | - | - | - | - | 49 |
| - | 1 | - | - | - | 5 |
| - | - | 1 | - | 1 | 3 |
| Total P.M.C. analysed | | | | | 57 |

II. S. simplicifolium Bitt. x S. Rybinii, Juz. et Buk.

The parents of this hybrid S. simplicifolium and S. Rybinii have 12 chromosomes as their haploid numbers. Here, again, there was no opportunity to study the mode of syndesis, but the genetical results tend to show (cf. pp. 78-84) that the mode of pairing is allosyndetic in this hybrid. The 12 chromosomes of simplicifolium pair with 12 chromosomes of Rybinii; and at diakinesis generally form 12 bivalents (Fig. 290). The pairing of chromosomes is not always complete (cf. Table XXXV). Thus out of 220 pollen-mother cells analysed at metaphase, 12 cells showed 11 bivalents and 2 univalents (Fig. 292).

TABLE XXXV.

Showing chromosome complement in 220 pollen-mother-cells of S. simplicifolium x Rybinii.

| Metaphase complement | Frequency | Figure |
|---|---|---|
| 12 bivalents | 200 | 291 |
| 11 bivalents and 2 univalents | 14 | 292,u.* |
| 12 bivalents and 1 fragment | 6 | 293,f.* |
| Total P.M.C. analysed | 220 | |

* u = univalent. f = fragment.

Fragmentation of chromosomes (Fig. 293,f) and non-orientation of bivalents has often been seen at metaphase. In Fig. 295, two bivalents which have failed to orientate at the equatorial region have been figured (in black).

At first division the bivalents disjoin regularly, leaving the univalents midway between the separating chromosome groups. The univalents may divide while lagging (Fig. 297) or be included intact in the groups at the poles. In Fig. 298 is shown the separation of 12-12 chromosomes to the poles together with one lagging half univalent ($u^1_1$). The equal distribution in this figure is more obvious than real, undoubtedly due to one half univalent having reached a pole and been included in the group; this is seen at $u_2$, in black. At the other pole there are eleven chromosomes plus one univalent. Table XXXVI shows the frequency of lagging univalents at anaphase.

TABLE XXXVI.

Showing frequency of lagging chromosomes at first anaphase in 96 pollen-mother-cells of S. simplicifolium x Rybinii.

| No. of P.M.C. showing clean separation | No. of laggards Unsplit 1 | Unsplit 2 | Split 1 | Split 2 | No. of P.M.C. showing other irregularities | Frequency |
|---|---|---|---|---|---|---|
| 80 | - | - | - | - | - | 80 |
| - | 1 | - | - | - | - | 3 |
| - | - | - | 1 | - | - | 4 |
| - | - | - | - | 2 | - | 1 |
| - | - | - | - | - | 8 | 8 |
| Total P.M.C. analysed | | | | | | 96 |

## TABLE XXXVII.

Showing frequency of chromatid bridges and fragments at first anaphase in 96 pollen-mother-cells of S. simplicifolium x Rybinii.

| No. of P.M.C. showing clean separation | No. of chromatid bridges | No. of fragments | No. of P.M.C. showing other irregularities | Frequency |
|---|---|---|---|---|
| 80 | - | - | - | 80 |
| - | 1 | 1 | - | 3 |
| - | 1 | - | - | 2 |
| - | - | 1 | - | 3 |
| - | - | - | 8 | 8 |
| Total P.M.C. analysed | | | | 96 |

A chromatid bridge and a fragment (f) have often been seen at anaphase (Fig. 296); the occurrence of these has been analysed in 96 pollen-mother-cells (Table XXXVII). Fig. 299 shows equal distribution of 12 chromosomes at either side at anaphase and in the figure the chromosomes are spaced out more than they are on the actual spindle.

Secondary associations were clearly observed at first metaphase (Fig. 294) but paucity of material prevented a detailed analysis. Such analysis was made on the abundant material of the second metaphase and the details are presented in figures 301-314 and Table XXXVIII.

### TABLE XXXVIII.

Showing character and frequency of secondary associations at second metaphase in <u>S</u>. <u>simplicifolium</u> x <u>S</u>. <u>Rybinii</u>.

| No. of single chromosomes | No. of chromosomes in groups of | | | | | Frequency | Figure |
|---|---|---|---|---|---|---|---|
| | 2 | 3 | 4 | 5 | 6 | | |
| 12 | - | - | - | - | - | 2 | 300 |
| 10 | 1 | - | - | - | - | 2 | 301 |
| 9 | - | 1 | - | - | - | 2 | 302 |
| 8 | 2 | - | - | - | - | 4 | 303 |
| 8 | - | - | 1 | - | - | 2 | 304 |
| 7 | 1 | 1 | - | - | - | 2 | 305 |
| 7 | - | - | - | 1 | - | 1 | 306 |
| 6 | 3 | - | - | - | - | 6 | 307 |
| 6 | 1 | - | 1 | - | - | 2 | 308 |
| 5 | 2 | 1 | - | - | - | 3 | 309 |
| 4 | 4 | - | - | - | - | 10 | 310 |
| 4 | 1 | 2 | - | - | - | 2 | 311 |
| 4 | - | 1 | - | 1 | - | 1 | 312 |
| 4 | 1 | - | - | - | 1 | 1 | 313 |
| 3 | 3 | 1 | - | - | - | 1 | 314 |
| Total P.M.C. analysed | | | | | | 41 | |

In this hybrid loculi of anthers containing pollen-mother-cells at second metaphases were conspicuous by reason of the presence of diploid pollen-mother-cells with 24 chromosomes (Fig. 315). The occurrence of these diploid metaphase plates only among cells showing second metaphase indicates that these are presumably due to the fusion of second metaphase plates. Müntzing (1933) in triploid <u>Solanum</u> and Karpechenko (1928) in the hybrid <u>Raphano-Brassica</u>, demonstrated the fusion of metaphase plates at second division. Fig. 316 shows the anaphase separation of

24 chromosomes at either side of the pole in a diploid cell, the chromosomes in the figure are widely spaced out.

The distribution of chromosomes at second metaphase was often unequal as might be expected owing to irregularity during first division.

The following distribution of chromosomes was noted on plates:

TABLE XXXIX.

Showing distribution of chromosomes on second metaphase plates in S. simplicifolium x Rybinii.

| No. of chromosomes on plates I | II | Frequency | Figure |
|---|---|---|---|
| 12 | 12 | 17 | 317 |
| 12 | 13 | 2 | 318 |
| 13 | 13 | 1 | 319 |
| 12 | 12 + 1 fragment | 1 | 320 |
| Total P.M.C. analysed | | 21 | |

In Fig. 320 portraying one of the second metaphase plates a small chromatin body is to be noted (outlined). This, on account of its size, can only be interpreted as a fragment. Generally the fragments are eliminated but in this case it was probably carried to the pole by the separating chromosomes at first anaphase.

At second anaphase a chromatid bridge is often seen (Figs. 321 and 322). Fig. 322 is provided to show a case of a chromatid bridge with a fragment (f) which is being eliminated. In Fig. 323 is shown a bridge and a lagging chromosome in a diploid cell.

Table XL shows the frequency of chromatid bridges, lagging and eliminated chromosomes. Lagging and elimination of chromosomes at this time is not rare (Figs. 325-327). In Fig. 324 is shown the separation of 11-11 chromosomes at either side with one lagging chromosome which is divided ($u^{1}_{1}$ and $u^{1}_{2}$), and two chromosomes which are eliminated ($el_1$ and $el_2$); whereas Fig. 325 shows lagging of one chromosome (u) in between the two separating groups of chromosomes at either side.

TABLE XL.

Showing frequency of chromatid bridges, fragments, lagging chromosomes and eliminated chromosomes at second anaphase in 61 pollen-mother cells of S. simplicifolium x Rybinii

| No. of P.M.C. showing clean separation | No. of P.M.C. showing bridges | No.of fragments | No.of laggards | | | | No of eliminated chromosomes | Frequency |
|---|---|---|---|---|---|---|---|---|
| | | | I | II | I | II | | |
| 39 | - | - | - | - | - | - | - | 39 |
| - | 1 | 1 | - | - | - | - | - | 4 |
| - | 1 | - | - | - | - | - | - | 1 |
| - | - | - | - | - | 1 | 1 | - | 2 |
| - | - | - | 1 | - | - | - | - | 6 |
| - | - | - | - | - | - | - | 1 | 6 |
| - | - | - | - | - | - | - | 2 | 3 |
| Total P.M.C. analysed | | | | | | | | 61 |

## 6. POLLEN.

Pollen formation in the species under consideration is not as regular as one would expect in diploid forms. In all the species where complete observation is possible "polycary" is frequently noted. The characteristic of this phenomenon is that extra nuclei are formed from chromosomes eliminated in fragmented parts or whole chromosomes. Dwarf and morphologically deformed pollen grains result in these cases owing to irregularity during division - a condition often observed in known hybrids.

TABLE XLI.

Showing morphologically deformed pollen in Solanum species and their hybrids.

| Species and Hybrids | Percentage of deformed pollen |
|---|---|
| S. lanciforme | 5.6 |
| S. Parodii | 12.6 |
| S. infundibuliforme | 12.0 |
| S. stenotomum var. | 48.2 |
| S. Rybinii | 21.6 |
| S. polyadenium | 6.3 |
| S. Parodii x infundibuliforme | 12.0 |
| S. simplicifolium x Rybinii | 81.9 |

Although Table XLI shows a fairly high percentage of morphologically good pollen in some of the species it is, however, to be emphasised that such apparent fertility may be misleading for Beeker (1939) showed that in Solanum demissum nearly half of the morphologically good pollen was nevertheless not viable.

It is noteworthy that in the hybrid S. Parodii x infundibuliforme, the unusual condition of apparently perfect pollen together with polycary is found (Fig. 328). On the other hand the hybrid simplicifolium x Rybinii showed a high percentage of deformed pollen (Fig. 329) the viability of which could not be tested.

Many known hybrids often have perfectly good pollen, for example Viola arvensis x tricolor (Clausen 1926), Avena sativa and the so-called "fatuoid mutants" of the obviously hybrid species (Huskins 1927) show a high degree of viable pollen in the presence of polycary. But in wheat hybrids Thompson (1926) has demonstrated that a high percentage of apparently good pollen will not germinate.

## 7. DISCUSSION.

These results may be discussed under four subheads - (I) Secondary association, (II) Chromatid-bridge formation, (III) Non-congression of bivalents, and (IV) Presence of univalents.

### (A). I. Secondary association.

There are two distinct kinds of associations which are seen in Solanum. First in point of time the primary association, arising from particulate attractions which lead to the pairing of chromosomes at zygotene. This primary association is manifested at first metaphase by maintenance of chiasmata formed at pachytene. Only chromosomes which are physically held by chiasmata survive the strong repulsion force operating at diakinesis. This force of repulsion continues until mid-diakinesis, when the intensity of the repulsion gradually diminishes, to disappear at pro-metaphase. When this repulsion-phase ends there is apparent another form of association, the secondary association which is the result of general "affinity" between different chromosomes which are phylogenetically related, and is not due to the persistance of any actual connections.

The associations of more than two chromosomes in polyploids at metaphase of meiosis was first observed by Kuwada (1910) in *Oryza sativa*. Later Darlington (1928) postulated the theory of secondary association from his observation on *Prunus*. Lawrence (1931b) reviewed the theory and considered that the secondary association arises at pro-metaphase and persists until the second repulsion-phase which in many plants is interkinesis, but where this stage is short a certain proportion of associations survive even at the second division. Here in the species under consideration the secondary association is observed extending from first to second metaphase and indeed survives until second anaphase (cf. Müntzing 1933).

Studies on the secondary association of chromosomes have led to interesting conclusions as to the primary basic number of certain genera. Darlington and Moffett (1930) in *Pyrus* and Moffett (1931) on the whole group of *Pomoideae* concluded that 17 was the secondary basic number derived from the primary basic number of 7 by replication of certain chromosomes in a set of seven.

Lawrence (1929 and 1931a) revealed that in *Dahlia* though the lowest haploid number of chromosomes in the genus is 16, the secondary associations of chromosomes indicate that ancestors with the haploid number of 8 chromosomes existed, but are now extin~~k~~ct. The author also inferred from the evidence in the literature that in several other genera, namely *Salix*, *Gossypium*, *Xanthium*, *Ficus*, *Vitis* and *Solanum*, with high basic numbers there are also secondary polyploids.

Observations on secondary association in most plants have often been difficult to interpret at first metaphase due to the presence of polyvalents caused by primary association. Here in the species under consideration primary associations of more than two chromosomes were not observed except in *S. stenotomum* where on one occasion a trivalent was seen and the frequency of such an association must be extremely low indeed. In these cases therefore the analysis of the secondary association at metaphase of both the divisions was comparatively simple although this was more pronounced at the second metaphase. From the amount of evidence of secondary association of chromosomes in "diploid" Solanum species, there is thus good reason for assuming as inferred by Lawrence (1931b) that the basic number of chromosomes in Solanum is 6. It is evident from Tables XLII and XLIII that in all the species the most frequent combination was 4 groups of 2 and 4 single chromosomes either at first or second metaphase. It is to be noted, however, that the maximum groups of two noted were 5.

Considering the basic number in Solanum as 6, the secondary association should theoretically lead to 6 groups each of 2 chromosomes, but this condition is only partially attained. It must be remembered that the invariable occurrence of such theoretical groups is only possible in the absence of competition (Darlington and Moffett 1930) and structural changes in the individual chromosomes.

TABLE XLII.

Showing for first metaphase in *Solanum* species the frequency of bivalents occurring grouped in two when the number of such groups may be one to five.

| Species | No. of plates examined | Frequency of bivalents in 5 | 4 | 3 | 2 | 1 groups of two | Frequency of groups other than two and groups of two in combination with them | Frequency of free bivalents |
|---|---|---|---|---|---|---|---|---|
| *S. lanciforme* | 136 | - | 31 | 26 | 24 | 12 | 28 | 15 |
| *S. Parodii* | 148 | 3 | 29 | 22 | 18 | 16 | 54 | 6 |
| *S. infundibuliforme* | 90 | - | 15 | 11 | 11 | 10 | 33 | 10 |
| *S. stenotomum* var. | 49 | 2 | 8 | 6 | - | 3 | 27 | 3 |
| *S. Rybinii* | 79 | - | 18 | 15 | 8 | 6 | 27 | 5 |
| *S. polyadenium* | 70 | - | 13 | 11 | 5 | 10 | 23 | 8 |

Secondary associations have been regarded by Lawrence (1931b) as the characteristic of allopolyploids. Allopolyploids between species which are not very closely related may have chromosomes which are only homologous in scattered portions of their length. Thus if ABC and DEF represent the haploid complements of two species whose number of pairing blocks if assumed is very small, it is likely that the chromosomes of the hybrid between ABC and DEF would hardly form any chiasmata since the chiasmata are proportional to the length of the paired chromosomes at pachytene

(Darlington and Mather 1932).

TABLE XLIII.

Showing for second metaphase in <u>Solanum</u> species and their hybrids the frequency of chromosomes occurring grouped in two where the number of such groups may be one to five.

| Species and hybrids | No. of plates examined | Frequency of chromosomes in groups of two | | | | | Frequency of groups other than two and groups of two in combination with them | Frequency of free chromosomes |
|---|---|---|---|---|---|---|---|---|
| | | 5 | 4 | 3 | 2 | 1 | | |
| <u>S.lanciforme</u> | 56 | - | 11 | 7 | 5 | 5 | 25 | 3 |
| <u>S.Parodii</u> | 153 | 5 | 30 | 23 | 21 | 13 | 54 | 7 |
| <u>S.infundibuliforme</u> | 93 | 4 | 17 | 12 | 14 | 6 | 36 | 4 |
| <u>S.stenotomum</u> var. | 81 | 3 | 24 | 17 | 7 | 6 | 19 | 5 |
| <u>S.Rybinii</u> | - | - | - | - | - | - | - | - |
| <u>S.polyadenium</u> | - | - | - | - | - | - | - | - |
| <u>S.Parodii</u> x <u>infundibuliforme</u> | 88 | 3 | 19 | 12 | 9 | 3 | 38 | 4 |
| <u>S.simplicifolium</u> x <u>Rybinii</u> | 41 | - | 10 | 6 | 4 | 2 | 17 | 2 |

Hence chiasmata will rarely be formed on regions paired over a short distance. The result of this would be production of diploid gametes. In the next generation primary pairing would most likely be autosyndetic, that is ABC will pair with ABC and DEF with DEF, and will form chiasmata since the number of pairing blocks of ABC and ABC or DEF and DEF are larger than those of ABC and DEF. The affinity of $\genfrac{}{}{0pt}{}{\text{ABC}}{\text{ABC}}$ and $\genfrac{}{}{0pt}{}{\text{DEF}}{\text{DEF}}$ although not strong enough to show primary association will attract each other and result in secondary association. Thus, for instance:

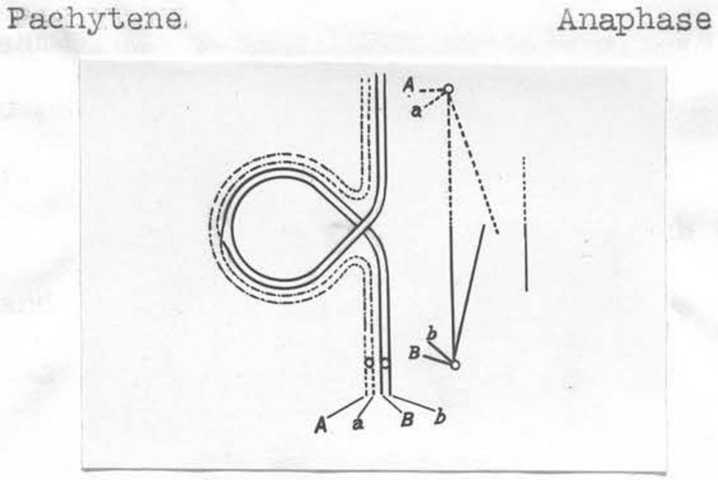
In the hybrid although ABC and DEF would hardly form any chiasmata they may have a chance of differentiation of their chromosomes by gene mutation or structural changes. Now suppose a certain segment of AA is interchanged with a segment of EE and a part of EE with CC. If the interchanged segments are very small they will not form any chiasmata to show their primary pairing, but the interchanged segments being homologous will attract each other and may result in secondary association of six chromosomes, for example

But in the face of competition between so many chromosomes it is quite possible these chromosomes will show secondary association in groups of 2, 3, 4 or even up to 5. Thus structural change of individual chromosomes might upset the theoretical expectancy, namely the secondary association of chromosomes only in groups of 2. In this regard it should be noted that Sikka (1940) demonstrated aberrant types of secondary association in Brassica nigra which he regarded as due to structural re-arrangements and complexities in the individual chromosomes.

### II. Chromatid-bridge formation, its consequence and the possibility of evolution of new chromosomes.

Chromatid bridges are frequently seen both in the species and in the hybrids under consideration and these may be explained on the basis of crossing-over within an inversion.

An inversion may be defined as a reversal of a segment which may take effect at the early stages of meiosis when chromosomes happen to fold over themselves, and break at the point of overlap and reunite in a different sequence.

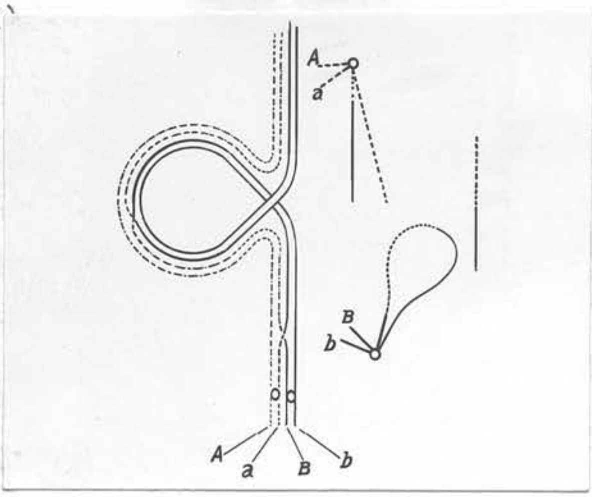


Text Fig. I.

In the pairing chromosomes Aa and Bb, if a section is inverted in the chromosome Bb, it will twist round and pair. Now if crossing-over occurs in the inverted region (Text Fig. 1) a continuous chromatid Ab with double centromeres, two normal chromatids A and B and a fragment formed partly from a and partly from b and without any centromere will be formed. The chromatid with two centromeres will form a bridge while the chromatids A and B with single centromere will separate normally and the fragment will be set free at first anaphase.

There is another possible way by which the bridge may not appear at first anaphase but be seen at second anaphase, namely, the continuous chromatid might pass to the same pole at first division leaving the fragments and would consequently form a bridge only at the second anaphase. The presence of fragments on the divisional plane at first anaphase without any bridge formation (cf. Figs. 122 and 175) taken together with the occurrence of bridges at the second anaphase suggests strongly that the continuous chromatid passes to the same pole during first division. This leads to the assumption that the "looped type" of configuration as described by Smith (1935) in *Trillium* is due to the presence of two cross-overs, one within the inversion region and another proximal to it involving one of the chromatids in both cross-overs. Such may occur in

Solanum, although this has not been found in the present investigation. Such a "looped type" of configuration when formed, would naturally pass to the same pole in the first division, leaving the fragment on the divisional plane and disjoin at the second division (Text Fig. II).



Text Fig. II.

In Lilium Richardson (1936) demonstrated a similar configuration at first anaphase and this separated at the second division.

Table XLIV shows that the inversion bridges occur in varying proportion in all the Solanum species studied. Upcott (1937b) in Tulipa and Mensinkai (1939) in Allium have correlated sterility with bridge formation. They classified their "inversion heterozygosity" into three classes on the basis of the frequency of bridges: (1) those that showed 10 per cent inversion or more, (2) those that showed less than 10 per cent, and (3) those that showed rare inversion, i.e. less than 1 per cent. Percentage of inversion as high as 10 per cent or more causes considerable sterility, whereas fertility in other groups (those showing less than 10 per cent of inversion) is not so much affected.

TABLE XLIV.

Showing percentage of chromatid bridges in *Solanum* species and their hybrids.

| Species and Hybrids | Percentage of bridges |
|---|---|
| *S. lanciforme* | 5.6 |
| *S. Parodii* | 8.1 |
| *S. infundibuliforme* | 1.9 |
| *S. stenotomum* var. | 25.6 |
| *S. Rybinii* | ? * |
| *S. polyadenium* | 9.1 |
| *S. Parodii* x *infundibuliforme* | 1.6 |
| *S. simplicifolium* x *Rybinii* | 13.3 |

* Bridges occur, but could not be analysed in large number of cells.

It is to be emphasised in this connection that the chromatid bridge may break at any point and thus give rise to chromosomes with additional segments or to chromosomes lacking certain parts. It is possible that such a new chromosome type may render the gamete containing it non-viable but this is not necessarily so for the degree to which such additional or missing segments affect function probably depends on size. Moreover, it may be argued that the unequal breaking and loss of fragments would not affect the polyploids to the same extent as the diploids since they may have compensating additions or deficiencies in other chromosomes. The new chromosome-type, however, should not bring out immediate phenotypic change, but serve rather as a basis on which future differentiation of types can take place.

### III. Non-congression of bivalents.

As mentioned earlier, one or two bivalents were seen to lie off the metaphase plate. These bivalents later may orientate on the equatorial plate of metaphase and divide regularly, but occasionally they fail to orientate themselves on the divisional plane and so lie off the spindle zone at anaphase. Darlington (1937) considered non-congression of bivalents as due to interchromosomal repulsion on a crowded plate, and possibly also to increased distance between the centromeres through long chromosomes having formed a single chiasma instead of three or four. The inordinate distance between the centromeres in such chromosomes decreases the repulsion which is believed to be the effective agent in the orientation of chromosomes on the metaphase plates. On this assumption, therefore, the rod-bivalents should be more liable to non-orientation than the ring-bivalents and in the present case the frequency of non-orientation of rod-bivalents was considerably higher than that of ring-bivalents a condition observed only in one instance (cf. Fig. 53).

In Phalaris caerulescens Parthasarathy (1939) observed non-orientation of ring-bivalents and regarded the delay in orientation in these as caused by the maldisposition of the axes of bivalents during the disappearance of the nuclear membrane and the determination of the spindle poles. The bivalents whose axes lie in the direction of the poles move more quickly to the equatorial plate than those whose axes are perpendicular to the poles.

## IV. The presence of univalents: its cause and consequence.

The occurrence of univalents at first metaphase in all the species and the artificial hybrids under consideration is not peculiar to Solanum. The presence of all the chromosomes in bivalents at metaphase in a large number of cases, however, shows that the univalents are homologous at least as to segments if not throughout their entire length. It is often considered that the failure of pairing among chromosomes which are potentially capable of doing so may be due to mechanical interference with pairing owing to the presence of too many homologous chromosomes (Gairdner and Darlington 1931, Moffett 1936b). On this hypothesis bivalents along with univalents would be expected in polyploid species with high chromosome number and it is indeed the case here. Along with the mechanical interference is to be considered the time-factor and the method of pairing; these influence to a great extent the retention of the connection formed at primary pairing. In species where the pairing is localised the time available for pairing is short and the pairing chromosomes may remain free at regions further from the point from which pairing begins. In such cases chiasmata would hardly be formed in small segments of paired chromosomes as they are proportional to the paired length of the chromosomes. This would possibly reduce the number of bivalents as chiasmata will not be formed to retain the connection of primary pairing at metaphase and the result will be the presence of univalents. Levan (1940) in tetraploid Allium has shown that the phenomenon of localisation of pairing may be regarded as one of the causes in reducing the multiple associations and the consequence is the presence of bivalents and univalents. A similar instance has also been recorded in Limonium rariflora O. Kuntze (Choudhuri 1942).

The cytological data obtained in regard to the species under consideration gives good reason to suppose that they are of hybrid origin (cf. pp 71-72). Failure of pairing in the hybrids in general in spite of the presence of pairable mates is characteristic.

The effects of hybridisation in reducing chromosome pairing are well known in Raphano-Brassica hybrids (Karpechenko 1928). The action of genetic factor has been assumed by Darlington and his co-workers (1937) in a number of instances, many of them are segregates from known hybrids. But it is only in Zea Mays (Beadle 1930) that this factor is known; it is the presence of a recessive gene which causes almost complete failure of pairing. It is probable that hybridisation in combination with genetic dissimilarity causes failure of pairing in Solanum.

The univalents which fail to orientate at first metaphase (as they do generally) behave in different ways. This is determined by the relative position of the univalents in relation to the equator of the spindle (cf. pp 15-16). In the first anaphase they may pass to the poles undivided or may split or divide while lagging. In Table XLV is shown the percentage of split and unsplit univalents at first division. The consequence of splitting and division of univalents is the presence of an unusually high number of chromosomes at second metaphase. This is quite a usual phenomenon in species and hybrids (viz. S. stenotomum var. and S. simplicifolium x Rybinii) where the percentage of split or divided univalents is high. The lagging univalents which at the end fail to reach the poles are either eliminated or form micronuclei.

At second anaphase lagging chromosomes are often seen. The univalents which pass intact to the poles at first division divide at second anaphase.

In *Nicotiana* univalents behave in a different way in different hybrids. Thus in *N. sylvestris* x *tabacum*, the univalents never divided at first anaphase (Goodspeed and Clausen 1927) whereas in *N. tomentosa* x *tabacum* (Goodspeed and Clausen 1928) the univalents frequently divided at first anaphase and consequently second metaphase exhibited more than the expected number of chromosomes.

TABLE XLV.

Showing percentage of unsplit and split univalents at first anaphase in *Solanum* species and their hybrids.

| Species and hybrids | Percentage of lagging univalents | First anaphase<br>Percentage of unsplit univalents | <br>Percentage of split or divided univalents |
|---|---|---|---|
| *S. lanciforme* | 9.5 | 7.1 | 2.4 |
| *S. Parodii* | 2.3 | 1.15 | 1.15 |
| *S. infundibuliforme* | 5.8 | 4.4 | 1.4 |
| *S. stenotomum* var. | 6.8 | 1.8 | 5.0 |
| *S. polyadenium* | 3.4 | 1.4 | 2.0 |
| *S. Parodii* x *infundibuliforme* | 6.6 | 3.3 | 3.3 |
| *S. simplicifolium* x *Rybinii* | 8.3 | 3.1 | 5.2 |

## (B). Species formation in Solanum.

It has been shown by Woodworth (1929) in Betula and Corylus, Sikka (1940) in Brassica and other authors in other species, that allo-polyploidy played an important role in the evolution of new species. The discovery of a complete polyploid series in potatoes (quoted from Bukasov 1933) leaves no doubt of the part played by polyploidy in speciation in Solanum. On the basis of the earlier works of Müntzing (1933), Ellison (1935) and the present investigation, it may be considered that the primary basic number in Solanum is 6. One obvious line of evolution in the potatoes is the establishment of amphidiploid forms with high chromosome numbers whose ancestors are not now known. The present-day "diploids" presumably belong to this class. Lawrence (1929 and 1931a) came to a similar conclusion about the genus Dahlia. There are also instances of natural amphidiploids whose parents are still in existence. The most notable example of this is Galeopsis Tetrahit the origin of which species is explained on the basis of chromosome doubling in the hybrid G. pubescens x speciosa. The artificial amphidiploids raised from G. pubescens x speciosa resemble the natural G. Tetrahit not only in external morphology but also in cytological behaviour. So these resemblances of this artificial form to the natural

G. Tetrahit were definite evidence of the genesis of the latter as from a cross between G. pubescens and G. speciosa or their progenitors (Müntzing 1932).

The investigation of the chromosomes of "diploid" species dealt with here has shown that there is good evidence for the assumption that they are of hybrid origin. It is well established that hybrids are characterised by meiotic irregularities. The question now arises, do these "diploid" species behave in any way like any of the known hybrids, for example Galeopsis- or Brassica-type? Failure of pairing in pairable chromosome mates and lagging and elimination of chromosomes frequently occur. Along with these irregularities the frequent formation of chromatid bridges may be regarded as characteristic of hybrids. Jensen (1936) in his work on the genus Rumex concluded that all these irregularities were characters diagnostic of a hybrid. Similar views have been expressed by several authors, for instance Church (1929) in certain Gramineae, Woodworth (1929) in Betulaceae and Hicks and Stebbins (1934) in Paeonia Smouthi.

## SECTION II.

## GENETICAL STUDIES IN WILD AND NATIVE-CULTIVATED POTATOES.

## CONTENTS

## INTRODUCTION.

Running parallel with these cytological investigations careful notes were made of various external features of the plants. It was hoped that in time such a body of genetical data would accumulate as to reinforce or question any conclusions arrived at on the basis of the cytological studies. Naturally, more time is required to bring such a genetical enquiry to fruition but despite the fact that only two seasons experiences are available, it is felt that the genetical results already to hand are of sufficient value to offer here. The results will be presented under the following heads: I. Leaf index. II. Simple _versus_ compound leaf. III. Wing structure. IV. Flower colour.

Questions of self- and cross-compatibility are also of importance not only for themselves but because of their bearing on the question of phylogeny and cytological make-up. Results on these problems will be included in a later section.

### A. I. LEAF INDEX.

The not unusual phenomenon of heterosis or the appearance of vigour in the $F_1$ hybrids greater than that of the parents of the cross is well shown in potatoes. Hybrid-vigour although manifest in the increased size of the whole phenotype, is in *Solanum* hybrids very conspicuous in regard to the leaves. The analysis of leaf indices of various species and interspecific hybrids of *Solanum* shows that the leaf indices of the $F_1$ families tend to exceed the arithmetical mean of their parents, and indeed in some cases exceeds the leaf-index of the larger parent.

TABLE I.

Showing leaf indices of *Solanum* hybrids and their parents.

| Species and hybrids | Leaf index | Mean leaf index of parents | Figure |
|---|---|---|---|
| S. *simplicifolium* | - 65.4 | | 1 |
| hybrid | - 63.1 | 57.8 | 2 |
| S. *Rybinii* | - 50.2 | | 3 |
| hybrid | - 58.1 | 56.2 | 4 |
| S. *demissum* | - 62.2 | | 5 |
| S. *commersonii* | - 56.4 | | 6 |
| hybrid | - 56.6 | 49.8 | 7 |
| S. *ajuscoense* | - 43.3 | | 8 |
| S. *commersonii* | - 56.4 | | |
| hybrid | - 46.1 | 54.0 | 9 |
| S. *chacoense* | - 52.0 | | 10 |
| S. *fendleri* | - 56.5 | | 11 |
| hybrid | - 76.7 | 59.3 | 12 |
| S. *demissum* | - 62.2 | | |
| S. *fendleri-demissum* | - 76.7 | | |
| hybrid | - 61.7 | 53.6 | 13 |
| S. *polyadenium* | - 42.1 | | 14 |

Table I shows the leaf indices of 8 species and 6 hybrids (Figs. 1-14). It is to be noted in this connection, however, that the hybrid between the two normal species *S. commersonii* and *S. chacoense* is dwarf in the extreme and as might be expected in this case the leaf index is far below the calculated parental mean. Groth (1912) working with tomatoes noted that in the cross between large and small fruited varieties, an average size between the two (i.e. the arithmetical mean) was never realised; in every case the fruit was smaller.

It may be that this S. commersonii x chacoense dwarf hybrid is chromosomically a numerically "unbalanced" type, and there is good evidence to support such an assumption since Rybin (1933) has observed very irregular distribution of chromosomes on the second metaphase plates of S. commersonii. Darlington and Moffett (1930) recorded the production of seedlings from "triploid" forms of Pyrus which were generally poor in development, abnormal in character and proven to be "unbalanced" chromosomically. Similar instances in Solanum hybrids are not rare as, for example, in the progenies of S. demissun x tuberosum (Beeker 1939). It is important to notice that this thesis of the "unbalanced" character of this hybrid receives confirmation from its complete sterility in $F_1$, no $F_2$ plants being possible.

In $F_2$ of S. Rybinii x demissum when the whole appearance of the leaf is examined, the various forms may be classified (Table II). These classes are four in number. (1) Those resembling the demissum parent. (2) Those resembling the Rybinii parent. (3) Those which resemble $F_1$ intermediate, and finally a class containing an "off-type". All these classes are shown in photographs (Figs. 15-18). It is seen that the new "off-type" differs from the three expected types in that it has lanceolate-type of leaflets and a larger number of folioles.

TABLE II.

Showing segregation of leaf type in the progenies of *S. Rybinii* x *demissum*.

| Ref. No. of plants | Intermediate type | *demissum* type | *Rybinii* type | "off-type" |
|---|---|---|---|---|
| | Leaf index | | | |
| 897a/1 | 57.2 | | | |
| 897a/4 | 54.2 | | | |
| 897a/6 | 57.2 | | | |
| 897b/6 | 58.1 | | | |
| 897a/3 | | 58.2 | | |
| 897a/7 | | 60.6 | | |
| 897b/1 | | 60.1 | | |
| 897a/5 | | | 50.6 | |
| 897a/4 | | | 52.7 | |
| 897b/2 | | | | 39.6 |
| 897b/3 | | | | 50.9 |
| 897b/5 | | | | 43.9 |
| Mean leaf index | 56.6 | 59.6 | 51.6 | 44.8 |
| Figure | 15 | 16 | 17 | 18 |

The production of these so-called off-types (Fig. 19) is of great interest and the development of any thesis to explain their origin must be left until a considerable amount of genetical and cytological analysis is completed. It may be that they are due merely to the sifting out of genes in a polymeric series or they may be due rather to some form of cytological segregation. *S. demissum* has three times the number of chromosomes that *S. Rybinii* has ("hexaploid" x "diploid" if the basal number is 12) and this at once provides a source of recombinations on a purely cytological basis.

TABLE III.

Showing segregation of leaf-type in the progenies of *S. fendleri* x *demissum*.

| Ref. No. of plants | Intermediate type | *demissum* type | *fendleri* type |
|---|---|---|---|
| | Leaf index | | |
| 891a/6 | 75.8 | | |
| 891a/1 | | 55.3 | |
| 891a/8 | | 67.3 | |
| 891a/2 | | | 62.1 |
| 891a/3 | | | 56.6 |
| 891a/7 | | | 57.7 |
| Mean leaf index | 75.8 | 61.3 | 58.8 |
| Figure | 20 | 21 | 22 |

The segregation of leaf-type has been noted in the progenies of two other hybrids and the details of these are in Tables III (Figs. 20-22) and IV (Figs. 23-26). It is apparent from the tables that the segregation in the two hybrids, *S. fendleri* x *demissum* and *S. fendleri-demissum* x *polyadenium* follows on the whole on a similar line as outlined above.

TABLE IV.

Showing segregation of leaf-type in the progenies of (*S. fendleri* x *demissum*) x *polyadenium*.

| Ref. No. of plants | Intermediate type | *demissum* type | *fendleri* type | *polyadenium* type |
|---|---|---|---|---|
| | Leaf index | | | |
| 893a/6 | 69.3 | | | |
| 893a/9 | 72.5 | | | |
| 893a/12 | 73.7 | | | |
| 893a/13 | | 61.4 | | |
| 893a/2 | | | 54.3 | |
| 893a/7 | | | 57.6 | |
| 893a/14 | | | | 50.0 |
| Mean leaf index | 71.8 | 61.4 | 55.9 | 50.0 |
| Figure | 23 | 24 | 25 | 26 |

## II. SIMPLE *versus* COMPOUND LEAF.

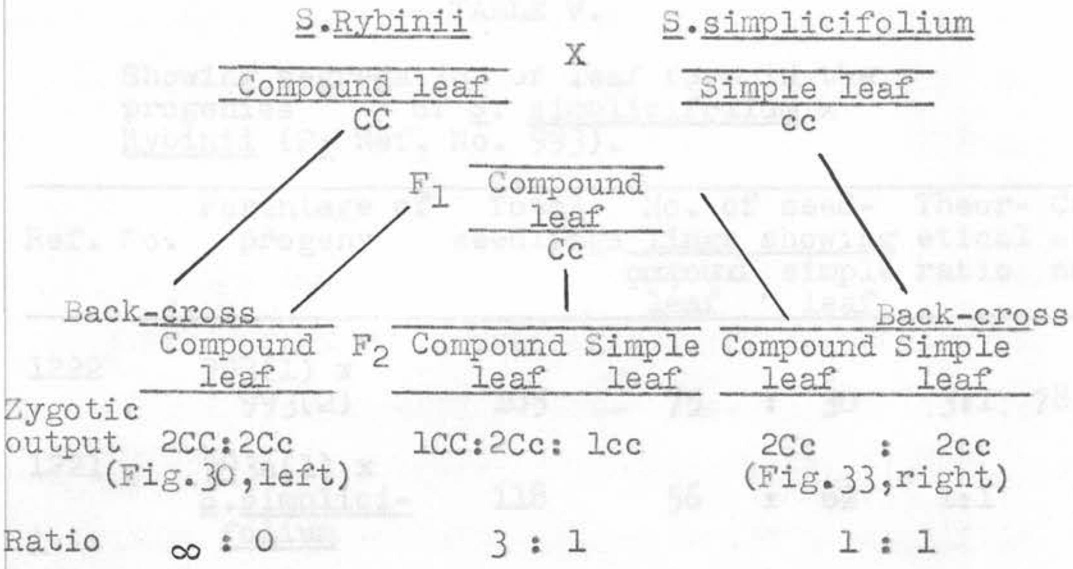
The work of Emme (1937) may be merely noted here in that he studied the phytogenetic relationships of three "diploid" species, namely *S. Rybinii* Juz.et Buk., *S. stenotomum* Juz. et Buk. and *S. goniocalyx* Juz. et Buk., but he did not analyse the leaf characters.

The two forms of leaves, the inheritance of which is under discussion here, are simple and compound.

The discovery of the simple form of leaf in a tuber-producing *Solanum* has afforded an opportunity to study the inheritance of leaf forms. *S. simplicifolium* Bitt. (Fig. 27) a wild species from Bolivia, is unique in known potatoes in that the leaf is simple (Fig. 1).

In the cross between S. simplicifolium and S. Rybinii (Fig. 28), all the offspring (Fig. 29) had compound leaves (Fig. 2) showing thereby that the compound form of leaf of S. Rybinii is dominant over the simple of S. simplicifolium. In the $F_2$ progenies the numbers of compound- and simple-leaf obtained in the seedling were 75 and 30 respectively (Figs. 30, right, and 33, left). This approaches the theoretical ratio of 3 compound- : 1 simple-leaf. Hence it is considered that the compound form of leaf is probably controlled by one factor C, then crossing with c (for simple leaf) would give Cc in $F_1$ and produce compound leaf. The $F_1$ hybrid, heterozygous for C factor, that is Cc, would produce offspring with the following genetic constitution at the ratio of 1 CC : 2 Cc : 1 cc. Plants with the constitution of CC and Cc phenotypically, however, would be similar and produce compound leaves since C is completely dominant over c.

The $F_1$ hybrid (Cc) when back-crossed with the recessive, S. simplicifolium (cc) produced seedlings with 56 compound- : 62 simple-leaves, which is a close approach to the theoretical ratio of 1 : 1. This ratio is expected on the basis of simple inheritance as shown before. Thus when Cc is crossed with cc, progenies with the following genetic constitution would be produced at the ratio of 2 Cc : 2 cc (i.e. 1 : 1) (cf. Text Fig. I).



Text Fig. I.

Back-crossing $F_1$ (Cc) with dominant S. Rybinii (CC) produced 61 compound- : 0 simple-leaf, this again satisfies the theoretical requirement of ∞ : 0 as expected. Thus Cc x CC would produce offspring with the genetic constitution of CC and Cc, so all plants would have compound leaves (cf. Text Fig. I).

In Table V is shown the details of observed, theoretical and calculated ratios in the $F_2$ and back-crossings.

TABLE V.

Showing segregation of leaf form in the progenies ( of *S. simplicifolium* x *Rybinii* ($F_1$ Ref. No. 993).

| Ref. No. | Parentage of progeny | Total seedlings | No. of seedlings showing compound leaf : simple leaf | Theoretical ratio | Calculated number |
|---|---|---|---|---|---|
| 1222 | 993(1) x 993(2) | 105 | 75 : 30 | 3:1 | 78.75:26.25 |
| 1221 | 993a(1) x *S.simplicifolium* | 118 | 56 : 62 | 1:1 | 59 : 59 |
| 1224 | 993a(4) x *S.Rybinii* | 61 | 61 : 0 | ∞:0 | 61 : 0 |

## III. WING STRUCTURE.

Many varieties of potatoes are characterised by lateral wings of tissue which extend longitudinally up and down the stem. In potato this wing structure can be divided into two classes, namely (1) broad-wing, and (2) rudimentary or practically no-wing. Broad-wing again may be sub-divided into two, (a) waved, and (b) plain wing. *S. simplicifolium* belongs to group (1,a) and *S. Rybinii* to group (2)as regards wing structure.

In the cross between *S. simplicifolium* and *S. Rybinii* the $F_1$ hybrid showed uniformly broad wing. Figs. 34-36 show the character of the wing structure of the parents and $F_1$ respectively. The appearance of only broad wings in the $F_1$ population showed that the broad wing is dominant over the rudimentary wing, and both S. simplicifolium and S. Rybinii can be regarded to be homozygous for the wing character.

Segregation of wing structure in $F_2$ is shown in Table VI. In an $F_2$ family of 105 plants, 80 had broad- and 25 rudimentary-wing. Here again it shows an approach to the theoretical ratio of 3 : 1. In that case the factorial constitution of S. simplicifolium as regards the wing structure may be described as WW. Mating with ww (S. Rybinii) produced an $F_1$ hybrid with the genetic constitution of Ww. $F_2$ population raised from plants with the constitution of Ww would produce offspring of the following genetic constitution at the ratio of 1 WW : 2 Ww : 1 ww. Seedlings with the constitution of WW and Ww would produce broad wing and ww rudimentary wing (Fig. 37, a and b).

In the back-cross of $F_1$ (Ww) with the recessive S. Rybinii (ww) were produced 61 offspring, of which 30 had broad wing and 31 rudimentary wing (cf. Table VI). This satisfies the theoretical ratio of 1 : 1. Thus Ww x ww would produce zygotes of genetic constitution Ww and ww at the ratio 1 : 1. Plants with the genetic constitution of Ww and ww would be broad- and rudimentary-winged respectively.

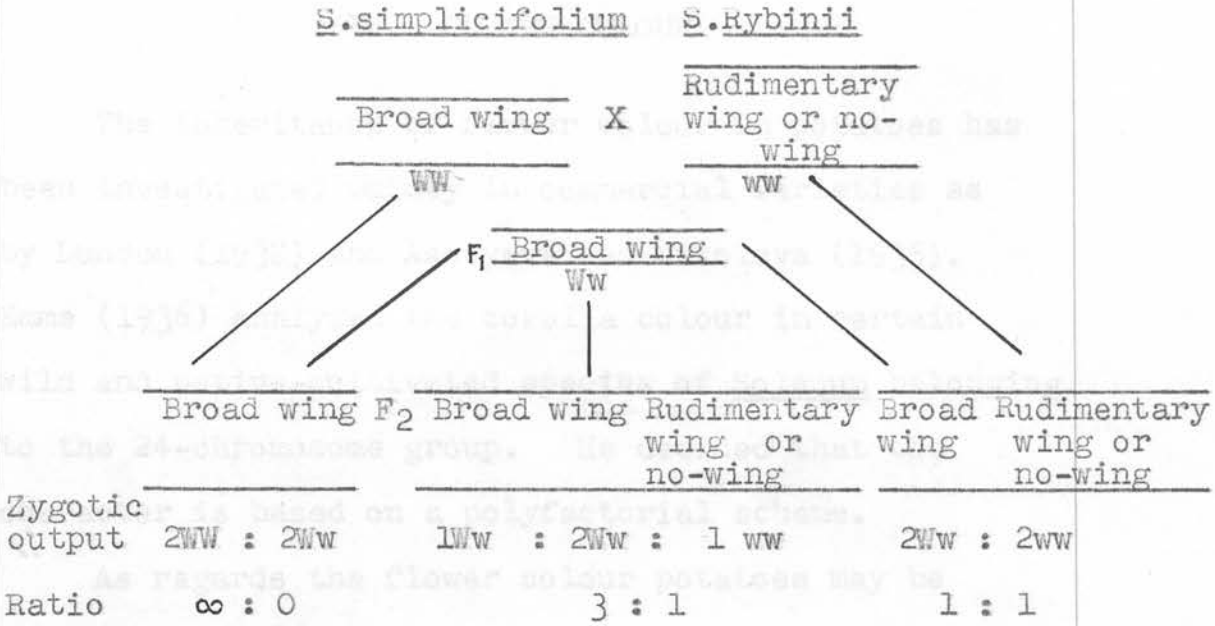
TABLE VI.

Showing segregation of wing structure in the progenies of S. simplicifolium x Rybinii ($F_1$ Ref. No. 993).

| Ref. No. | Parentage of progeny | Total seedlings | No. of seedlings showing broad wing : wing absent | Theoretical ratio | Calculated number |
|---|---|---|---|---|---|
| 1222 | 993(1) x 993(2) | 105 | 80 : 25 | 3:1 | 78.75:26.25 |
| 1224 | 993a(4) x S.Rybinii | 61 | 30 : 31 | 1:1 | 30.5 :30.5 |
| 1221 | 993a(1) x S.simplicifolium | 116 | 116 : 0 | ∞ :0 | 116 : 0 |

$F_1$ (Ww) when back-crossed with the dominant S. simplicifolium (WW) produced 116 plants all of which were broad-winged and this conforms to the ratio of ∞: 0 demanded by theory (cf. Table VI). Thus Ww x WW would produce offspring only with the genetic constitution WW and Ww. Hence all the plants would be broad-winged.

The factorial segregation as regards the wing structure in $F_2$ and back-crossings are shown in the Text Fig. II.


S.simplicifolium
S.Rybinii
Broad wing
X
Rudimentary wing or no-wing
WW
ww
F1 Broad wing
Ww
Broad wing
F2
Broad wing
Rudimentary wing or no-wing
Broad wing
Rudimentary wing or no-wing
Zygotic output
2WW : 2Ww
1Ww : 2Ww : 1 ww
2Ww : 2ww
Ratio
∞ : 0
3 : 1
1 : 1

Text Fig. II.

## IV. FLOWER COLOUR.

The inheritance of flower colour in potatoes has been investigated mainly in commercial varieties as by Lunden (1932) and Asseyeva and Nikoleva (1935). Emme (1936) analysed the corolla colour in certain wild and native-cultivated species of Solanum belonging to the 24-chromosome group. He decided that the character is based on a polyfactorial scheme.

As regards the flower colour potatoes may be classified into two main groups, (1) coloured, (2) white. The coloured group may again be divided into three sub-groups: (a) red-purple, (b) blue-purple and (c) blue. The colour intensity in the coloured groups ranges from very faint to deep. It is presumed that the difference in colour intensity is due to differences in genotype (Lunden 1932 and 1937). Blue-purple colour is considered to be due to the presence of both red-purple and blue.

The white-flowered group may again be sub-divided into two groups: (a) "pure" white and (b) "tinted" white (Salaman 1926). The latter possesses a slight colour usually confined to the under surface of the petals. This colour sometimes fades away as the flower ages. The genetics of these "tinted white" flowers has not been sufficiently investigated and they have often been included in the white group (Asseyeva and Nikoleva 1935). Such amalgamation of "tinted" and "pure" white is indefensible and when authors have taken this course the work is largely invalidated. Black (1930) in crossing "tinted white" with "pure white" flowers obtained offspring with "tinted white" and "pure white" flowers. Thus it seems that tinted-whites which have some colour on the under surface of petals cannot be considered as white, and this is presumably controlled by a definite factor or factors.

In a cross between "tinted" white (with reddish-purple tinge) flowered S. Rybinii and blue-purple flowered S. demissum, the $F_1$ hybrid produced blue-purple flowers. Segregation of flower colour in $F_2$ progenies is shown in Table VII. Out of 68 plants in an $F_2$ family, 46 produced blue-purple, 18 red-purple, 2 blue and 2 white flowers. It is to be noted here that the flowers of the last-mentioned group were true whites and had no colour on the under surface of petals (cf. Table VIII). If all the coloured flowers (including "tinted" white) are grouped in one class and the true whites in the other, then the ratio of coloured and non-coloured flowers comes to 66:2. This approaches the theoretical ratio of 63:1. Analysis of the progeny shows that 64 of the plants had "red" colour in the flowers and 4 were non-red.

TABLE VII.

Showing segregation of flower colour in the $F_2$ and back-cross progenies of *S. Rybinii* x *demissum* ($F_1$ Ref. No. 735).

| Parentage | Total Seedling | No. of plants *BP : RP : B : Wh | Theoretical ratio | Calculated number |
|---|---|---|---|---|
| $F_1$ selfed | 68 | 46 : 18 : 2 : 2 | 45:15:3:1 | 48:16:3:1 |
| 735 x *S. Rybinii* | 14 | 8 : 6 : - : - | 1:1 | 7:7 |

* BP = Blue-purple.
RP = Red-purple
B = Blue
Wh = White

This closely approaches a 15:1 ratio and suggests that two factors controlling the "red" are present. Similarly 48 plants had blue colour in the flowers and 20 were non-blue, indicating a 3:1 ratio and a single factor inheritance. It may therefore be considered that the blue-purple flower of the $F_1$ hybrid is controlled by three factors. Since *S. Rybinii* has slight colour on the under surface of the petals it seems reasonable to think that one of the colour factors in the $F_1$ hybrid is supplied by *S. Rybinii*. Let it be designated $R^1$. The remaining two colour factors of the $F_1$ hybrid must have come from *S. demissum*. If we denote the factor $R^2$ for red-purple and B for blue then the combination of both factors may produce blue-purple flowers as red is masked by the presence of blue

(Lunden 1932, 1937). In other words blue-purple is "epistatic" to red. The constitution of blue-purple flowers of S. demissum may be considered as $R^2R^2BB$. The factor $R^2$ is slightly different from $R^1$ in reaction of flower colour. $R^1$ alone produces slight colour on the under surface of petals, has cumulative effect with $R^2$ and produces pale blue-purple in combination with B, whereas $R^2$ alone produces a more intense colour over a larger area and in combination with B produces a deeper blue-purple colour. On this assumption the genetic constitution of the "tinted white" flowers of S. Rybinii with reddish-purple tinge on the under surface of petals may be considered as $R^1R^1$. Thus a cross with "tinted" white and blue-purple flowered S. Rybinii and S. demissum respectively will produce an $F_1$ hybrid with the genetic constitution $R^1r^1R^2r^2Bb$. Plants with such constitution will produce blue-purple flowers since blue-purple is "epistatic" to red.

The $F_1$ hybrids heterozygous for $R^1$, $R^2$ and B (i.e. $R^1r^1R^2r^2Bb$) factors will produce gametes of the following genetic constitution:

(1) $R^1R^2B$, (2) $R^1R^2b$, (3) $R^1r^2B$, (4) $R^1r^2b$,
(5) $r^1R^2B$, (6) $r^1R^2b$, (7) $r^1r^2B$, and (8) $r^1r^2b$.

Table VIII shows the zygotic output in the $F_2$ progenies. As is to be expected the flowers in $F_2$ families differ a great deal in colour intensities owing to their different genetic constitution.

## TABLE VIII.

Showing zygotic output in the $F_2$ progenies of S. Rybinii x demissum and formulae for different flower colour.

| Genetic constitution of zygotes | | | | | | | |
|---|---|---|---|---|---|---|---|
| No. of zygotes | Blue-purple flowers | No. of zygotes | Red-purple flowers | No. of zygotes | Blue flowers | No. of zygotes | White flowers |
| 1 | $R^1R^2B$<br>$R^1R^2B$ | 1 | $R^1R^2b$<br>$R^1R^2b$ | 1 | $r^1r^2B$<br>$r^1r^2B$ | 1 | $r^1r^2b$<br>$r^1r^2b$ |
| 2 | $R^1R^2B$<br>$R^1R^2b$ | 2 | $R^1R^2b$<br>$R^1r^2b$ | 2 | $r^1r^2B$<br>$r^1r^2b$ | | |
| 2 | $R^1R^2B$<br>$R^1r^2B$ | 1 | $R^1r^2b$<br>$R^1r^2b$ | | | | |
| 4 | $R^1R^2B$<br>$R^1r^2b$ | 2 | $R^1R^2b$<br>$r^1R^2b$ | | | | |
| 2 | $R^1R^2B$<br>$r^1R^2B$ | 4 | $R^1r^2b$<br>$r^1R^2b$ | | | | |
| 4 | $R^1R^2B$<br>$r^1R^2b$ | 2 | $R^1r^2b$<br>$r^1r^2b$ | | | | |
| 4 | $R^1R^2B$<br>$r^1r^2B$ | 1 | $r^1R^2b$<br>$r^1R^2b$ | | | | |
| 8 | $R^1R^2B$<br>$r^1r^2b$ | 2 | $r^1R^2b$<br>$r^1r^2b$ | | | | |
| 1 | $R^1r^2B$<br>$R^1r^2B$ | | | | | | |
| 2 | $R^1r^2B$<br>$R^1r^2b$ | | | | | | |
| 2 | $R^1r^2B$<br>$r^1r^2B$ | | | | | | |
| 4 | $R^1r^2b$<br>$r^1r^2B$ | | | | | | |
| 1 | $r^1R^2B$<br>$r^1R^2B$ | | | | | | |
| 2 | $r^1R^2B$<br>$r^1R^2b$ | | | | | | |
| 2 | $r^1R^2B$<br>$r^1r^2B$ | | | | | | |
| 4 | $r^1R^2b$<br>$r^1r^2B$ | | | | | | |
| Total 45 | | 15 | | 3 | | 1 | |

Thus the blue-purple flowers may have sixteen different genetic constitutions, whereas red-purple flowers may have eight and blues may have two different constitutions (cf. Table VIII). In Table IX. is shown the genetic constitution of two extreme shades in each of the three flower colour classes, blue-purple, red-purple and blue flowers.

TABLE IX.

Showing genetic formulae for different shades of blue-purple, red-purple and blue flowers.

| Blue-purple flowers | | Red-purple flowers | | Blue flowers. | |
|---|---|---|---|---|---|
| Dark | Pale | Dark | "Tinted" | Dark | Pale |
| $R^1R^1R^2R^2BB$ | $R^1r^1r^2r^2Bb$ | $R^1R^1R^2R^2bb$ | $R^1r^1r^2r^2bb$ | $r^1r^1r^2r^2BB$ | $r^1r^1r^2r^2Bb$ |

In the back-cross of the $F_1$ hybrid with S. Rybinii, a family of 14 plants was obtained. In these 14 plants 8 produced blue-purple flowers and 6 produced red-purple flowers. This satisfies the theoretical ratio of 1:1. Thus in a cross $R^1r^1R^2r^2Bb$ x $R^1R^1r^2r^2bb$ zygotes with the following constitutions will be produced as shown in Table X.

TABLE X.

Showing zygotic output in the $R^1r^1R^2r^2Bb$ x $R^1R^1r^2r^2bb$ and the resulting flower colour.

| Zygotes | Flower colour | |
|---|---|---|
| $R^1R^2B$<br>$R^1r^2b$ | Blue-purple | |
| $R^1R^2b$<br>$R^1r^2b$ | Red-purple | |
| $R^1r^2B$<br>$R^1r^2b$ | Blue-purple | |
| $R^1r^2b$<br>$R^1r^2b$ | Red-purple | 4 Blue-purple<br>:<br>4 Red-purple |
| $r^1R^2B$<br>$R^1r^2b$ | Blue-purple | |
| $r^1R^2b$<br>$R^1r^2b$ | Red-purple | |
| $r^1r^2B$<br>$R^1r^2b$ | Blue-purple | |
| $r^1r^2b$<br>$R^1r^2b$ | Red-purple | |

## B. SELF- AND CROSS-COMPATIBILITIES.

A number of authors have studied various diversified genera from the point of view of elucidating the fertility of the various members when pollinated in different relationships. These studies amongst them have had threefold aims. Firstly, to elucidate the genetic mechanism controlling the various degrees of fertility; secondly, to establish degrees of relationship and possible phylogenetic lines, and thirdly, to provide data for the constructive plant-breeder about to attempt the synthesis of new plants.

The technique of experiments may have varied in detail but all rely on protecting individual flowers from uncontrolled pollination and then ensuring either self-pollination of entire flowers or deliberate cross-pollination of emasculated flowers. The methods of protection of flowers have always been those which permitted fertility in fertile relationships.

The methods adopted here were those proved successful in routine potato breeding, namely, isolation of the individual plants in a special plant-breeder's greenhouse.

Treating first with self-compatibility in Solanum, it is to be noted that apart from data on the cultivated commercial varieties there is very little information to be derived from the literature. This is to be regretted as the "diploid" species brought from the wild or from native cultivations overseas are likely to supply the gene complex of our cultivated varieties with many allelomorphs of useful characters such as resistance to disease, early-maturity, high protein content etc.

In Table XI is given the results of selfing several "diploid" Solanum species and their varieties. The number of flowers pollinated and the berries produced are noted in one column whereas the average number of seeds per berry is given in a separate column. It is apparent from Table XI that out of 16 species and one variety selfed only one species (viz. S. polyadenium) produced seeds. Stout (1926) reported on the self- and cross-incompatibility in S. chacoense and S. Jamesii and his results are in agreement with the data obtained from these species in the present investigation. At this stage it may be useful to insist that as regards these "diploid" potatoes the self-compatibility results are very similar to those obtained in many other genera.

As regards cross-compatibility between the various forms again it must be noted that literature yields very few data. Pal and Pushkar Nath (1942) studied the genetic nature of self- and cross-incompatibility in sixteen varieties of S. Caldasii and one variety of S. subtilis. The authors regarded self- and cross-incompatibility as inherited characters and considered

## TABLE XI.

Showing results of selfing "diploid" species of Solanum.

| | Species | F.P./B* | Average seed per berry |
|---|---|---|---|
| | S. simplicifolium | 7/0 | |
| | S. goniocalyx | 7/0 | |
| | S. boyacense | 6/0 | |
| | S. Kesselbrenneri | 7/0 | |
| + | S. phureja | 6/0 | |
| | S. Rybinii | 7/0 | |
| | S. Parodii | 9/0 | |
| | S. infundibuliforme | 6/0 | |
| | S. stenotomum var. E.P.C. 1104 | 9/0 | |
| | ~~S.~~ longipedicellat~~um~~a ~~var.~~ E.P.C. 12 | 8/8 | 76·5 |
| | S. polyadenium | 5/5 | 115.8 |
| | S. lanciforme | 6/0 | |
| + | S. Jamesii | 10/0 | |
| + | S. chacoense | 7/0 | |
| x | S. ajanhuri ~~var.~~ E.P.C. 126 | 7/0 | |
| xx | S. ajanhuri ~~var.~~ P.S. 28 | 7/0 | |
| ø | E.P.C. 144 | 13/0 | |

* F.P. = No. of flowers pollinated.
B. = No. of berries.

\+ Self-incompatibility reported by other authors.
x Flower colour - Blue-purple.
xx Flower colour - Red-purple
ø An un-named species.

that at least five sterility allelomorphs, viz. $S^1$, $S^2$, $S^3$, $S^4$ and $S^5$ in a multiple allelomorphic series operated in various pair combinations to determine the self- and cross-incompatibility.

TABLE XII.

Showing results of crossing "diploid" species of *Solanum*.

| Mating |  |  | F.P./B | Average seeds per berry |
|---|---|---|---|---|
| Seed parent |  | Pollen parent |  |  |
| *S. simplicifolium* | x | *Rybinii* | 9/5 | 22.6 |
| do. | x | *boyacense* | 4/2 | 4.0 |
| do. | x | *goniocalyx* | 4/4 | 20.2 |
| do. | x | *Kesselbrenneri* | 4/2 | 11.0 |
| do. | x | *phureja* | 5/3 | 38.0 |
| do. | x | *stenotomum* var. E.P.C. 1104 | 3/2 | 18.5 |
| *S. Jamesii* | x | *simplicifolium* | 4/4 | 9.0 |
| do. | x | *lanciforme* | 14/9 | 5.3 |
| *S. chacoense* | x | *Rybinii* | 3/1 | 15.0 |
| *S. goniocalyx* | x | *boyacense* | 3/3 | 596.3 |
| do. | x | *Kesselbrenneri* | 3/3 | 396.6 |
| do. | x | *phureja* | 2/1 | 445.0 |
| do. | x | *Rybinii* | 6/1 | 11.0 |
| do. | x | *simplicifolium* | 2/1 | 437.0 |
| do. | x | *longipedicellatum* E.P.C. 12 | 4/1 | 212.0 |
| do. | x | E.P.C. 144 * | 4/4 | 516.7 |
| *S. Kesselbrenneri* | x | *boyacense* | 5/3 | 127.0 |
| do. | x | *chacoense* | 4/2 | 74.0 |
| do. | x | *goniocalyx* | 4/3 | 74.0 |
| do. | x | *simplicifolium* | 3/2 | 71.0 |
| do. | x | *Parodii* | 5/1 | 80.0 |
| do. | x | E.P.C. 144 | 4/3 | 126.0 |
| *S. phureja* | x | *goniocalyx* | 3/3 | 65.0 |
| do. | x | *Rybinii* | 2/1 | 264.0 |
| do. | x | *simplicifolium* | 3/2 | 201.0 |
| do. | x | *Parodii*. | 2/1 | 113.0 |
| do. | x | E.P.C. 144 | 2/2 | 193.0 |
| *S. polyadenium* | x | *lanciforme* | 4/1 | 8.0 |
| *S. Rybinii* | x | *boyacense* | 2/1 | 305.0 |
| do. | x | *Kesselbrenneri* | 4/2 | 445.5 |
| do. | x | *simplicifolium* | 2/1 | 391.0 |

TABLE XII (continued)

| Mating | | F.P./B | Average seeds per berry |
|---|---|---|---|
| Seed parent | Pollen parent | | |
| *S. longipedicellatum* E.P.C.12 | x *boyacense* | 3/2 | 8.0 |
| do. | x *goniocalyx* | 3/3 | 1.0 |
| do. | x *Kesselbrenneri* | 9/5 | 6.0 |
| do. | x *phureja* | 3/3 | 9.3 |
| do. | x *Rybinii* | 5/5 | 25.2 |
| do. | x *simplicifolium* | 3/3 | 3.6 |
| do. | x *Parodii* | 3/3 | 10.3 |
| do. | x *infundibuliforme* | 4/2 | 102.5 |
| do. | x E.P.C. 144 | 6/9 | 51.1 |
| *S. Parodii* | x *boyacense* | 5/4 | 135.7 |
| do. | x *goniocalyx* | 5/1 | 43.0 |
| do. | x *Kesselbrenneri* | 4/4 | 75.0 |
| do. | x *phureja* | 5/3 | 74.3 |
| do. | x *Rybinii* | 4/4 | 170.5 |
| do. | x *simplicifolium* | 3/1 | 54.0 |
| do. | x *infundibuliforme* | 4/4 | 244.5 |
| do. | x E.P.C. 144 | 5/4 | 228.0 |
| *S. infundibuliforme* | x *boyacense* | 6/1 | 133.0 |
| do. | x *goniocalyx* | 4/4 | 156.5 |
| do. | x *Kesselbrenneri* | 3/1 | 16.0 |
| do. | x *phureja* | 8/1 | 55.0 |
| do. | x *Rybinii* | 4/3 | 66.6 |
| do. | x *simplicifolium* | 3/1 | 228.0 |
| do. | x *Parodii* | 2/2 | 179.5 |
| do. | x E.P.C. 144 | 3/1 | 216.0 |
| *S. ajanhuri* var. E.P.C.126 | x *boyacense* | 2/2 | 64.0 |
| do. | x *goniocalyx* | 3/2 | 44.5 |
| do. | x *phureja* | 2/1 | 42.0 |
| do. | x *Rybinii* | 4/2 | 76.0 |
| do. | x *simplicifolium* | 3/2 | 76.5 |
| do. | x *Parodii* | 3/2 | 41.0 |
| do. | x E.P.C. 144 | 3/3 | 53.3 |
| E.P.C.144 | x *boyacense* | 3/2 | 179.0 |
| do. | x *goniocalyx* | 3/2 | 99.0 |
| do. | x *Kesselbrenneri* | 2/2 | 164.0 |
| do. | x *phureja* | 3/1 | 53.0 |
| do. | x *Rybinii* | 4/2 | 160.0 |
| do. | x *simplicifolium* | 3/2 | 83.5 |
| *S. ajanhuri* var. P.S.28 | x *goniocalyx* | 1/1 | 200.0 |
| do. | x *Kesselbrenneri* | 3/2 | 234.0 |
| do. | x *Rybinii* | 4/4 | 91.5 |
| do. | x *simplicifolium* | 4/2 | 152.0 |
| *S. stenotomum* var E.P.C.1104 | x *goniocalyx* | 6/1 | 102.0 |
| do. | x *Rybinii* | 4/2 | 68.5 |

* E.P.C. 144 - A new "diploid" species.

Table XII shows the results of intercrosses between various Solanum species. It is to be emphasised here that there is, however, some variation in degree in fertility (i.e. production of seeds) in reciprocal crosses. Thus S. simplicifolium is not so fertile with Rybinii or phureja pollen, while S. Rybinii and S. phureja react very well with simplicifolium pollen. There are a good many instances of similar nature which have been noticed in the present cross-compatibility experiments and these have also been recorded in Table XIII. Nelson (1927) had similar results in his work in Brassica. Thus the "Savoy" was not so fertile with cabbage pollen or with foreign "Savoy" pollen whereas cabbage reacted to "Savoy" at least as well as to pollen from another cabbage. It is hardly necessary to discuss this table further and at length, but it may be pointed out that a species behaving as a "good" seed parent in one of their relationships need not necessarily be good in another relationship. For example, S. Rybinii pollinated from S. Kesselbrenneri gives full fertility (with highest number, 445.5 seeds per berry, of all the crosses) but it is sterile in the reciprocal cross. When, however, S. Rybinii is used as a female parent in a cross with S. Parodii sterility appears whereas in the reciprocal fertility appears.

## TABLE XIII.

Showing differences in fertility
in reciprocal crosses in *Solanum*

| Mating<br>Seed parent | Pollen parent | No. of berries | Total seeds | Average seeds per berry |
|---|---|---|---|---|
| (*S.goniocalyx* | x *Kesselbrenneri* | 3 | 1190 | 396.6 |
| (*S.Kesselbrenneri* | x *goniocalyx* | 3 | 222 | 74.0 |
| (*S.goniocalyx* | x *simplicifolium* | 1 | 437 | 437.0 |
| (*S.simplicifolium* | x *goniocalyx* | 4 | 81 | 20.2 |
| (*S.goniocalyx* | x *longipedicellatum* E.P.C. 12 | 1 | 212 | 212.0 |
| (*S.longipedicellatum* E.P.C. 12 | x *goniocalyx* | 3 | 3 | 1.0 |
| (*S.goniocalyx* | x *phureja* | 1 | 445 | 445.0 |
| (*S.phureja* | x *goniocalyx* | 3 | 195 | 65.0 |
| (*S.goniocalyx* | x E.P.C.144 | 4 | 2067 | 516.7 |
| (E.P.C. 144 | x *goniocalyx* | 2 | 198 | 99.0 |
| (*S.phureja* | x E.P.C. 144 | 2 | 386 | 193.0 |
| (E.P.C. 144 | x *phureja* | 1 | 53 | 53.0 |
| (*S.phureja* | x *Parodii* | 1 | 113 | 113.0 |
| (*S.Parodii* | x *phureja* | 3 | 223 | 74.3 |
| (*S.Kesselbrenneri* | x *simplicifolium* | 2 | 142 | 71.0 |
| (*S.simplicifolium* | x *Kesselbrenneri* | 2 | 22 | 11.0 |

Reciprocal differences with opposite results have frequently been noted in cross-pollination experiments in "diploid" potatoes. In Table XIV and text figure III (p. 101) have been shown the results obtained in such cross-compatible experiments. East and Mangelsdorf (1925 and 1926) in *Nicotiana* reported similar reciprocal differences in cross-relations and they regarded this phenomenon as due to the fact that one genotype was heterozygous for the $S'$ allelomorph

(S = sterility) and the other genotype was homozygous for the allelomorphic pair. Thus $S_aS_a$ x $S_aS_b$ was cross-compatible on account of the fertilisation of $S_a$ ovules by $S_b$-bearing pollen but $S_aS_b$ ♀ x $S_aS_a$ ♂ was cross-incompatible. Anderson and Winton (1931) also noted that a particular self-incompatible *Nicotiana alata* did not cross as a seed parent with plants of *N. Langsdorfii* but did so as a male parent. It was assumed by the authors that the unusual *N. alata* had one special incompatibility factor "$S_F$" which prevented the functioning of any pollen of *N. Langsdorfii*.

TABLE XIV.

Showing opposite reactions in
reciprocal crosses in *Solanum*.

| Mating | | | Cross reactions * |
|---|---|---|---|
| Seed parent | | Pollen parent | + or o |
| (*S.Rybinii* | x | *Kesselbrenneri* | + |
| (*S.Kesselbrenneri* | x | *Rybinii* | o |
| (*S.Parodii* | x | *simplicifolium* | + |
| (*S.simplicifolium* | x | *Parodii* | o |
| (*S.Parodii* | x | *Rybinii* | + |
| (*S.Rybinii* | x | *Parodii* | o |
| (*S.Parodii* | x | *goniocalyx* | + |
| (*S.goniocalyx* | x | *Parodii* | o |
| (*S.Parodii* | x | E.P.C. 144 | + |
| (E.P.C. 144 | x | *S. Parodii* | o |
| (*S.longipedicellatum*, E.P.C. 12 | x | *Parodii* | + |
| (*S.Parodii* | x | *longipedicellatum*, E.P.C. 12 | o |
| (*S.ajanhuri*, E.P.C. 126 | x | *Parodii* | + |
| (*S.Parodii* | x | *ajanhuri*, E.P.C. 126 | o |
| (*S.ajanhuri*, E.P.C. 126 | x | *goniocalyx* | + |
| (*S.goniocalyx* | x | *ajanhuri*, E.P.C. 126 | o |

TABLE XIV (continued)

| Mating<br>Seed parent Pollen parent | Cross Reactions*<br>+ or o |
|---|---|
| (S.ajanhuri, E.P.C. 126 x Rybinii | + |
| (S.Rybinii x ajanhuri, E.P.C. 126 | o |
| (S.ajanhuri, E.P.C.126 x E.P.C. 144 | + |
| (E.P.C. 144 x ajanhuri, E.P.C. 126 | o |
| (E.P.C. 144 x Rybinii | + |
| (S.Rybinii x E.P.C. 144 | o |
| (S.infundibuliforme x Rybinii | + |
| (S.Rybinii x infundibuliforme | o |
| (S.longipedicellatum, E.P.C.12 x infundibuliforme | + |
| (S.infundibuliforme x longipedicellatum, E.P.C.12 | o |
| (S.longipedicellatum, E.P.C.12 x E.P.C.144 | + |
| (E.P.C. 144 x S.longipedicellatum, E.P.C.12 | o |

* + = compatible
o = incompatible

In crossing two self-incompatible species of Solanum, viz. S. simplicifolium and S. Rybinii a progeny of 8 plants was obtained. All the sister plants of the $F_1$ hybrids are self-incompatible. They are all cross-compatible with the female parent (S. simplicifolium) excepting plant No. 3 whereas all excepting plants No. 4 and 6 are cross-compatible (Table XV) with the male parent (S. Rybinii).

| ♀ \ ♂ | Rybinii | simplicifolium | infundibuliforme | Kesselbrenneri | goniocalyx | phureja | ajanhuri E.P.C.126 | boyacense | stenotomum var. E.P.C.1104 | Parodii | E.P.C.144 | Jamesii | polyadenium | lanciforme | chacoense | longipedicellatum, E.P.C. 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. Rybinii | O | F | S | F | S | S | S | F | S | S | S | S | S | S | S | S |
| 2. simplicifolium | F | O | . | F | F | F |  | F | F | S |  | S | S | S | S | S |
| 3. infundibuliforme | F | F | O | F | F | F | . | F | . | F | F | S | S | S | S | S |
| 4. Kesselbrenneri | S | F | . | O | F | S | S | F | S | F | F | S | S | S | f | S |
| 5. goniocalyx | F | F | . | F | O | F | S | F | S | S | F | S | S | S | S | S |
| 6. phureja | F | F | . | . | F | O | . | . | . | F | F | S | S | S | . | S |
| 7. ajanhuri E.P.C.126 | F | F | . | S | F | F | O | F | . | F | F | S | S | S | S | S |
| 8. boyacense | . | . | . | . | . | . | . | O | . | . | . | . | S | . | . | . |
| 9. stenotomum var. E.P.C.1104 | F | . | . | S | F | . | S | . | O | . | S | S | S | S | . | S |
| 10. Parodii. | F | F | F | F | F | F | S | F | S | O | F | S | S | S | S | S |
| 11. E.P.C.144 | F | F | S | F | F | F | S | F | S | S | O | S | S | S | S | S |
| 12. Jamesii | S | S | S | S | S | S | S | S | S | S | S | O | S | S | S | S |
| 13. polyadenium | S | S | S | S | S | S | S | S | S | S | S | S | F | S | S | S |
| 14. lanciforme | S | S | S | S | S | S | S | S | S | S | S | S | S | O | S | S |
| 15. chacoense | f | S | . | . | . | . | . | . | . | . | . | S | S | . | O | . |
| 16. longipediccelatum E.P.C.12. | f | S | S | f | f | f | . | f | . | f | f | S | S | S | S | ~~O~~ F |

1-9 – Tuberosa. 10 & 15 – Commersoniana. 12-14 – Pinnatisecta

Text Figure III.

Showing self- and cross-relations in various "diploid" species of Solanum. F = self- or cross-compatible; O = self-incompatible; S = cross-incompatible; and f = partially compatible, viability not tested. Blank space indicates that seeds not harvested yet and . shows incomplete data.

## TABLE XV.

Showing results of crossing of sister plants of $F_1$ progenies (No. 1-8) of *S. simplicifolium* x *Rybinii* and their cross-relations with their parents.

| Mating |  | *F.P./B. | Remarks |
|---|---|---|---|
| ♀ | ♂ |  |  |
| *simplicifolium* | x 1 | 3/3 | Good seeds |
| do. | x 2 | 3/1 | do. |
| do. | x 3 | 5/0 | Neither berries nor seeds |
| do. | x 4 | 4/3 | Good seeds |
| do. | x 5 | 2/2 | Berries too small yet, may produce good seeds. |
| do. | x 6 | 3/2 | Good seeds |
| do. | x 7 | 3/3 | do. |
| do. | x 8 | 3/2 | do. |
| *Rybinii* | x 1 | 2/1 | Berry too small yet, may produce good seeds. |
| do. | x 2 | 3/3 | Good seeds. |
| do. | x 3 | - | - |
| do. | x 4 | 2/0 | Neither berries nor seeds. |
| do. | x 5 | - | - |
| do. | x 6 | 2/0 | Neither berries nor seeds. |
| do. | x 7 | 2/1 | Good seeds. |
| do. | x 8 | - |  |
| 1 | x *simplicifolium* | 3/3 | Good seeds |
| 1 | x *Rybinii* | 4/1 | do. |
| 1 | x 1 | 2/0 | Neither berries nor seeds. |
| 1 | x 2 | 7/6 | Good seeds |
| 1 | x 3 | 7/2 | do. |
| 1 | x 4 | 4/3 | do. |
| 1 | x 5 | 6/2 | Berries too small yet, may produce good seeds |
| 1 | x 6 | 5/4 | Good seeds |
| 1 | x 7 | 3/3 | do. |
| 1 | x 8 | 6/0 | Neither berries nor seeds. |
| 2 | x *simplicifolium* | 4/2 | Big berries, no seeds. |
| 2 | x *Rybinii* | 3/3 | Seeds rather flat; doubtful viability; embryos can be seen. |
| 2 | x 1 | 5/5 | Big berries, no seeds. |
| 2 | x 2 | 4/0 | Neither berries nor seeds. |
| 2 | x 3 | 3/0 | do. do. |
| 2 | x 4 | 9/9 | Big berries, no seeds. |
| 2 | x 5 | 6/0 | Neither berries nor seeds. |
| 2 | x 6 | 6/0 | do. do. |
| 2 | x 7 | 7/0 | do. do. |
| 2 | x 8 | 4/4 | Big berries,no seeds. |

## TABLE XV (continued)

| Mating<br>♀ ♂ | F.P./B. | Remarks |
|---|---|---|
| 3 x *simplicifolium* | 8/2 | Big berries, no seeds |
| 3 x *Rybinii* | 4/4 | Seeds rather flat; doubtful viability; embryos can be seen. |
| 3 x 1 | 4/4 | do. do. |
| 3 x 2 | 3/0 | Neither berries nor seeds. |
| 3 x 3 | 4/0 | do. do. |
| 3 x 4 | 3/3 | Seeds rather flat; doubtful viability; embryos can be seen. |
| 3 x 5 | 4/0 | Neither berries nor seeds. |
| 3 x 6 | 4/0 | do. do. |
| 3 x 7 | 3/0 | do. do. |
| 3 x 8 | 4/4 | Seeds rather flat; doubtful viability; embryos can be seen. |
| 4 x *simplicifolium* | 3/3 | Good seeds. |
| 4 x *Rybinii* | 4/3 | do. |
| 4 x 1 | 3/3 | do. |
| 4 x 2 | 2/2 | do. |
| 4 x 3 | 16/0 | Neither berries nor seeds. |
| 4 x 4 | 4/0 | do. do. |
| 4 x 5 | 3/3 | Good seeds. |
| 4 x 6 | 3/3 | do. |
| 4 x 7 | 3/3 | do. |
| 4 x 8 | 3/3 | do. |
| 5 x *simplicifolium* | 7/2 | Seeds rather flat; doubtful viability; embryos can be seen. |
| 5 x *Rybinii* | 6/6 | do. do. |
| 5 x 1 | 5/5 | do. do. |
| 5 x 2 | 3/0 | Neither berries nor seeds. |
| 5 x 3 | 5/0 | do. do. |
| 5 x 4 | 5/4 | Seeds rather flat; doubtful viability; embryos can be seen. |
| 5 x 5 | 6/0 | Neither berries nor seeds. |
| 5 x 6 | 4/0 | do. do. |
| 5 x 7 | 4/0 | do. do. |
| 5 x 8 | 5/5 | Seeds rather flat; doubtful viability; embryos can be seen. |

TABLE XV (continued)

| Mating ♀ ♂ | F.P./B. | Remarks |
|---|---|---|
| 6 x *simplicifolium* | 5/5 | Big berries, no seeds. |
| 6 x *Rybinii* | 10/7 | Seeds rather flat; doubtful viability; embryos can be seen. |
| 6 x 1 | 5/5 | do. do. |
| 6 x 2 | 4/0 | Neither berries nor seeds. |
| 6 x 3 | 4/0 | do. do. |
| 6 x 4 | 4/2 | Big berries, no seeds. |
| 6 x 5 | 3/0 | Neither berries, nor seeds. |
| 6 x 6 | 3/0 | do. do. |
| 6 x 7 | 4/0 | do. do. |
| 6 x 8 | 4/4 | Seeds rather flat; doubtful viability; embryos can be seen. |
| 7 x *simplicifolium* | 5/4 | do. do. |
| 7 x *Rybinii* | 4/4 | do. do. |
| 7 x 1 | 3/3 | Big berries, no seeds. |
| 7 x 2 | 3/0 | Neither berries nor seeds. |
| 7 x 3 | 3/0 | do. do. |
| 7 x 4 | 4/2 | Seeds rather flat; doubtful viability; embryos can be seen. |
| 7 x 5 | 3/0 | Neither berries nor seeds. |
| 7 x 6 | 2/0 | do. do. |
| 7 x 7 | 4/0 | do. do. |
| 7 x 8 | 3/3 | Seeds rather flat; doubtful viability; embryos can be seen. |
| 8 x *simplicifolium* | 7/7 | Big berries, no seeds. |
| 8 x *Rybinii* | 3/3 | do. do. |
| 8 x 1 | 2/0 | Neither berries nor seeds. |
| 8 x 2 | 3/3 | Big berries, no seeds. |
| 8 x 3 | 3/3 | do. do. |
| 8 x 4 | 4/1 | Big berry, do. |
| 8 x 5 | 4/4 | Big berries, do. |
| 8 x 6 | 4/4 | do. do. |
| 8 x 7 | 4/1 | Big berry, do. |
| 8 x 8 | 4/0 | Neither berries nor seeds. |

* F.P. = No. of flowers pollinated.
B. = No. of berries.

Baur (1919) in crossing two self-incompatible Antirrhinum hispanicum obtained a progeny of 31 plants. All of them were cross-compatible with the female parent and about half were cross-incompatible with the male parent. Gruber (1932) in hybridising two self-incompatible species of Antirrhinum, viz. A. Ibanyezii and A. glutinosum obtained mostly self-incompatible progenies. The appearance of few self-compatible plants in the $F_1$ generation was regarded by him as due to some error or pseudo-fertility.

In cross reactions in sister plants of $F_1$ hybrids it is noted that there are broadly two groups of plants (Text Fig. IV, p. 106). Thus Group I on the one hand comprises plants No. 1 and 4 and Group II, on the other hand, comprises plants No. 2,3,5,6,7 and 8. Group I crosses as a female parent with all the sister plant pollen (viz. pollen of plants No. 1,2,4,5,6,and 7) excepting pollen of plants No. 3 and 8. While group II hardly produces good seeds as a female parent. It seems that the group II plants are showing one-way incompatibility although this cannot be definitely proved until the seeds of doubtful viability are tested. Sirks (1926) in Verbascum phoeniceum found one-way incompatibility to be frequent. Crane and Lawrence (1931) in discussing the one-way incompatibility suggested that since the chromosome number in

| ♀ \ ♂ | *Rybinii* | *simplicifolium* | 1 | 4 | 3 | 6 | 8 | 2 | 5 | 7 |
|---|---|---|---|---|---|---|---|---|---|---|
| *Rybinii* | O | F | F | S | . | S | . | F | . | F |
| *simplicifolium* | F | O | F | F | S | F | F | F | F | F |
| * 1 | F | F | O | F | F | F | S | F | F | F |
| * 4 | F | F | F | O | S | F | F | F | F | F |
| ** 3 | f | s | f | f | O | S | f | S | S | S |
| ** 6 | f | s | f | s | S | O | s | S | S | S |
| ** 8 | s | s | s | s | s | s | O | s | s | s |
| ** 2 | f | s | s | s | S | S | s | O | S | S |
| ** 5 | f | f | f | f | S | S | f | S | O | S |
| ** 7 | f | f | s | f | S | S | f | S | S | O |

* 1 and 4 (Group I).
** 3,6,8,2,5 and 7 (Group II).

Text Figure IV.

Showing self- and cross-relations in the sister plants of $F_1$ progenies of *S. simplicifolium* x *Rybinii* and with their parents. F = self- or cross-compatibility, seeds good; O = self-incompatible; S = cross-incompatible, no berries; s = cross-incompatible, berries but no seeds; and f = partially compatible, seeds of doubtful viability.

V. phoeniceum is 32, it is possibly a tetraploid and this is to be expected from a species of polyploid nature. For example pollen tubes carrying the sterility factors $S^1S^1S^2S^3$ may be compatible on a style having the factors $S^1S^1S^2S^2$ owing to the presence of the $S^3$ factor in the constitution of the pollen.

## DISCUSSION.

It would not be proper to embark on a full discussion of these compatibility results at this stage of the investigation, that must wait until results from the whole genus are available and these will take a long time to obtain. As regards phylogeny certain trends may be observed. Depending on the causal mechanism underlying incompatibility such a result indicates either close relationship or non-relationship. When the lack of either fruitfulness or fertility is due to a gene complex of the $S^1$----$S^n$ oppositional factor type then close relationship is indicated. When, on the other hand, the non-effect of pollen is due to total inhibition of pollen germination or cytological dissimilarity then lack of relationship may be inferred.

Adopting this view and noting that in these experiments no species belonging to the Pinnatisecta group crosses with any member of either of the other two groups involved, namely Tuberosa or Commersoniana, it may be inferred that Pinnatisecta is not closely related to the other two. The fact that Tuberosa and Commersoniana species freely intercross suggests a close relationship between them.

So too, cases of false-fruiting — the production of fully-developed fruits containing no developed ovules — must be accepted as showing physiological relationship, phylogenetic in character but with fertility barred by some cytological dissimilarity on the part of the parents.

The cases of what have been called "one-way-fertility", namely fertility between two species when one is the seed parent and sterility when the other is the seed parent, must too be taken to indicate phylogenetic "consanguinity" but with a definite cytological dissimilarity between the parents.

The whole appearance of the results from these compatibility studies reminds one of similar results from other genera such as those got by Crane and Lawrence (1931) with cherries, apples and other fruits, Sirks (1926) in Verbascum and so on. In every one of these cases it has been shown that an oppositional factor or multiple allelomorphic series was operating complicated by a heteroploid cytological position and there seems no reason but to assume that the same obtains in Solanum especially when one connects these results with the results given in the section dealing with cytological results. If, as the cytological evidence indicates, these *Solanum* "diploid" species are really allo-tetraploids with a basic number of 6 then the results such as those got from the *S. simplicifolium* x *Rybinii* mating become comprehensible.

## SUMMARY.

### SECTION I. (CYTOLOGY OF SPECIES AND HYBRIDS).

### I. CHROMOSOME NUMBER IN SPECIES AND HYBRIDS.

1. The chromosome number of the species of *Solanum*, and their hybrids, investigated are:-

| Species and hybrids | Chromosome number n |
|---|---|
| Solanum lanciforme Rydb. | 12 |
| * " Parodii sp. coll. Juz. et Buk. | 12 |
| " infundibuliforme Phil. | 12 |
| " stenotomum var. Juz. et Buk. | 12 |
| * " Rybinii Juz. et Buk. | 12 |
| " polyadenium Greenman | 12 |
| " Parodii sp. coll. Juz. et Buk. x infundibuliforme Phil | 12 |
| " simplicifolium Bitt. x Rybinii Juz. et Buk. | 12 |

* Haploid number of 12 chromosomes reported by other authors.

### II. MEIOSIS IN SPECIES.

2. The mid-diplotene stage is reported on in *S. Rybinii* only and here the bivalents show various configurations and interstitial chiasmata.

3. In all the species under consideration, although at first metaphase 12 bivalents are usually noted in their haploid nuclei, often 1 bivalent is represented by 2 univalents resulting in 11 bivalents and 2 univalents. The frequency of univalents is noted in tables.

4. Polyvalents do not occur except in S. stenotomum var. where one trivalent in the form of a chain is noted: the frequency of this is very low.

5. Fragmentation of chromosomes is often seen at first metaphase. The fragment is traced in S. Parodii from as early as diakinesis.

6. The univalents behave on the whole in a similar way in all the species. They either pass to the poles undivided or lag and divide. The division of univalents causes unequal distribution of chromosomes at second metaphase. The frequency of lagging univalents is noted in tables.

7. The univalents when eliminated (i.e. fail to be included in the daughter nuclei) form micronuclei.

8. The formation of a chromatid-bridge at first and second anaphase is found to be a usual phenomenon in all the species under consideration. The significance of the chromatid-bridge, its bearing on the evolution of new chromosomes and on sterility is discussed.

9. Formation of diploid pollen-mother-cells with 24 chromosomes is noted in *S. infundibuliforme*.

10. Irregularities at second division are noted.

## III. MEIOSIS IN HYBRIDS.

11. In the hybrids, *S. Parodii* x *infundibuliforme* and *S. simplicifolium* x *Rybinii* pairing is allosyndetic forming 12 bivalents. The number of bivalents is variable with consequent presence of univalents, viz. 11 bivalents and 2 univalents.

12. The univalents in the hybrids behave in the o/ same way at first metophase as in the species, i.e. either reaching the poles intact or dividing while lagging in the equatorial region.

13. A chromatid-bridge is noted both at first and second division.

14. Pollen-mother-cells with diploid number of 24 chromosomes are frequently seen in the hybrid *S. simplicifolium* x *Rybinii*.

15. At second anaphase lagging and elimination of chromosomes are noted.

## IV. SECONDARY ASSOCIATION.

16. The character and frequency of secondary association has been analysed in all the species and hybrids. In all cases the highest frequency of

4 groups of 2 and 4 free chromosomes is noted. On the basis of secondary association of chromosomes the basic number in Solanum is considered as 6 not 12.

## V. POLLEN.

17. In species and hybrids morphologically deformed pollen is seen together with morphologically "good" pollen.

## SECTION II. (GENETICAL STUDIES)

18. The leaf indices of various species and hybrids are recorded. The leaf indices of $F_1$ hybrids generally tend to exceed the arithmetical mean between the leaf indices of their parents.

19. It is suggested that the inheritance of leaf form in S. Rybinii and S. simplicifolium is controlled by a single factor, viz. C, where C produces the compound form of the leaf and which is dominant over simple leaf.

20. The wing structure in S. simplicifolium and S. Rybinii is controlled by a single factor, viz. W, which produces broad wing and the broad wing is dominant over absence of wing.

21. It is suggested that the "tinted" white flower of S. Rybinii with reddish-purple tinge on the under surface of the petals is controlled by a single factor, viz. $R^1$. The blue-purple flower of S. demissum is controlled by two factors, viz. $R^2$ and B. It is presumed that the factor $R^1$ is slightly different from $R^2$ in reaction of flower colour; when alone it produces slight reddish-purple tinge on the under surface of petals, has an intensified effect with $R^2$ and produces blue-purple when in combination with B. $R^2$ alone produces a more intense colour over a larger area and in combination with B produces deeper blue-purple colour. The factor B alone produces blue colour and is "epistatic" to red.

22. The results of self- and cross-compatibility are recorded in tables. The indication of "one-way" incompatibility in the sister plants of $F_1$ progenies of S. simplicifolium x Rybinii, and its significance is discussed.

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