CYTOLOGICAL STUDIES IN COTTON.

III. A HYBRID BETWEEN *GOSSYPIUM DAVIDSONII* KELL. AND *G. STURTII* F. MUELL.

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(With Plate XVI and Nine Text-figures.)

CONTENTS.

I. INTRODUCTION.

THE parental species of the *Gossypium* hybrid discussed here are both wild types which have never been cultivated. *Gossypium Davidsonii* is a native of Lower California and Mexico, while *G. Sturtii* is only found in Australia. Ecologically, both are xerophytes.

In both parents, the haploid chromosome number (n) is 13 (Harland, 1932; Longley, 1933; Skovsted, 1933), and the two species belong to groups which are geographically separated; cytologically, they are distinguishable by the sizes of their chromosomes (Skovsted, 1934). The chromosomes of *G. Davidsonii* are small, while those of *G. Sturtii* are much larger: a hybrid between these two species therefore possesses a special cytological interest.

II. TECHNIQUE.

The same cytological technique was employed as that described elsewhere (Skovsted, 1933 and 1934). In one respect only has an improvement been introduced, *i.e.* whereas earlier fixations of the root tips were made in Navashin's solution, later fixations were made in Lewitsky's chromic acid-formalin fixative (8 chromic acid to 2 formalin) (Lewitsky, 1931), since this shows the shape of the somatic chromosomes much better than Navashin's solution.

The hybrids were produced by using *G. Davidsonii* as female. Of ten crosses, only four produced ripe bolls containing in all forty seeds.

TABLE I.

*A comparison between the main features of the hybrid and its parents.*

	G. Davidsonii	G. Sturtii	Hybrid
Cotyledons	Entire	Notched	Intermediate
Hairiness	Hairy	Smooth	Smooth
Presence of wax	Absent	Present	Present, but less than in G. Sturtii especially in the rainy season
Leaf shape	Cordate	Ovate-deltoid	Intermediate
Glands on stem and leaves	Small	Large	Intermediate
Bracts	With teeth	Entire	With teeth but smaller than G. Davidsonii
Calyx	Entire	With teeth	With teeth but smaller than G. Sturtii
Corolla colour	Bright yellow	Mauve	Pale mauve
Pollen colour	Yellow	White	Pale yellow
Flowering season in Trinidad	The whole year	End of dry season (March–May)	The whole year
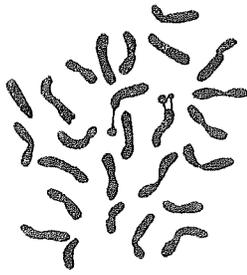
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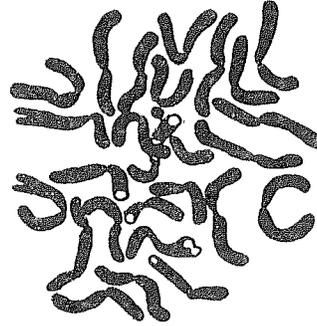
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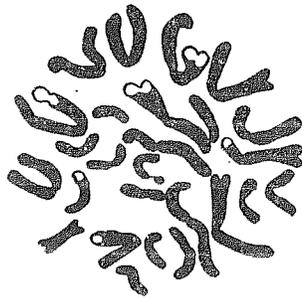
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Text-figs. 1–3. The somatic chromosomes of *Gossypium Davidsonii* and *G. Sturtii* and their hybrid (× 4700).

Text-fig. 1. *G. Davidsonii* with 26 small chromosomes.

Text-fig. 2. *G. Sturtii* with 26 larger chromosomes.

Text-fig. 3. The hybrid with 13 small and 13 larger chromosomes.

Germination proved difficult, and was not influenced either by treatment with sulphuric acid, or by removal of the seed coats. Eventually, by removing the seed coats, washing in sterile water, and then sowing in sterile cultures of 5 per cent. dextrose-agar, fourteen plants were obtained.

TABLE II.

*Showing chromosome conjugation in forty pollen mother cells in the hybrid G. Davidsonii × G. Sturtii.*

| No. of different combinations found	Univalents		Bivalents			Trivalents		Quadrivalents	No. of times observed
	S	D	S-D	S-S	D-D	S-S-D	D-S-D	D-S-S-D	
1	12	12	1	.	.	.	.	.	2
2	11	11	2	.	.	.	.	.	2
3	11	10	1	.	.	.	1	.	1
4	10	12	1	1	.	.	.	.	1
5	10	10	3	.	.	.	.	.	2
6	9	11	2	1	.	.	.	.	1
7	9	10	2	.	.	1	.	.	1
8	9	9	2	1	1	.	.	.	1
9	9	9	4	.	.	.	.	.	5
10	9	7	4	.	1	.	.	.	2
11	8	8	5	.	.	.	.	.	4
12	8	8	3	1	1	.	.	.	1
13	8	7	4	.	.	.	1	.	1
14	7	7	6	.	.	.	.	.	1
15	7	5	6	.	1	.	.	.	1
16	6	6	5	1	1	.	.	.	1
17	6	6	7	.	.	.	.	.	1
18	5	5	6	.	.	.	.	1	1
19	5	5	6	1	1	.	.	.	3
20	5	5	8	.	.	.	.	.	1
21	4	6	7	1	.	.	.	.	1
22	4	4	9	.	.	.	.	.	1
23	4	4	7	1	1	.	.	.	1
24	3	3	10	.	.	.	.	.	3
25	3	2	6	1	2	1	.	.	1
Totals	300	298	190	11	12	2	2	1	

D = Davidsonii, S = Sturtii.

III. OBSERVATIONS.

The hybrid, under Trinidad conditions, tends to be weakly and is smaller than either parent. Phenotypically, it is approximately intermediate, although some of the characters from both parents show incomplete dominance (Table I). So far it has been completely sterile, both in pollen and in eggs, whether selfed or in back-crosses with *G. Davidsonii*.
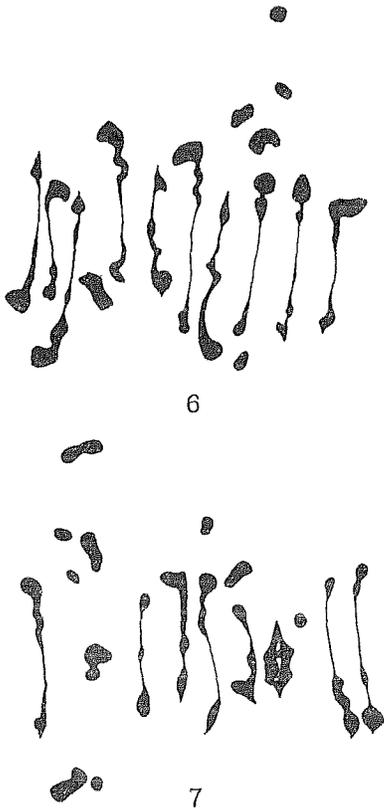
The somatic chromosomes of the parental species show a distinct difference both in length and in diameter, with a corresponding difference in volume. The distinction between the somatic chromosomes is maintained in the hybrid (Text-figs. 1–3).
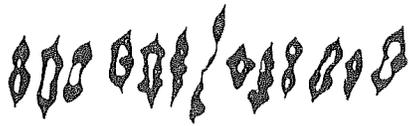
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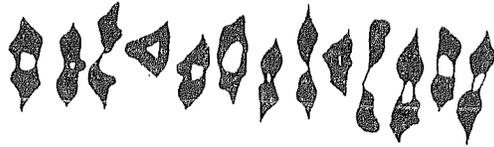
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Text-figs. 4–8. Side-views of metaphases from the first meiotic division in the two species and their hybrid (× 3100).

Text-fig. 4. *G. Davidsonii* with 13 small chromosomes.

Text-fig. 5. *G. Sturtii* with 13 larger chromosomes.

Text-fig. 6. The hybrid showing ten allosyndetic bivalents and six univalents.

Text-fig. 7. The hybrid showing six allosyndetic and two autosyndetic bivalents, and ten univalents (from left to right)*: 1 II (*D-S*); 7 I (3 *D* + 4 *S*); 1 II (*D-D*); 2 II (*D-S*); 2 I (1 *D* + 1 *S*); 1 II (*D-S*); 1 II (*S-S*); 1 I (*D*); 2 II (*D-S*).

Text-fig. 8. The hybrid showing two bivalents (1 *S-S*, and 1 *D-S*), and twenty-two univalents.

* The letters *D* and *S* are used respectively for a *Davidsonii* and a *Sturtii* chromosome.

The meiotic chromosomes of the two species also show a considerable difference in size (Text-figs. 4, 5, and Plate XVI, figs. 1, 2). In the meiotic divisions of the hybrid, it is fairly easy to distinguish the chromosomes of *G. Davidsonii* from those of *G. Sturtii* (Text-figs. 6–8 and Plate XVI, figs. 3, 4). The chromosome conjugation varies considerably from one pollen mother cell to another, and therefore the conjugation has been studied statistically by analysing forty complete pollen mother cells
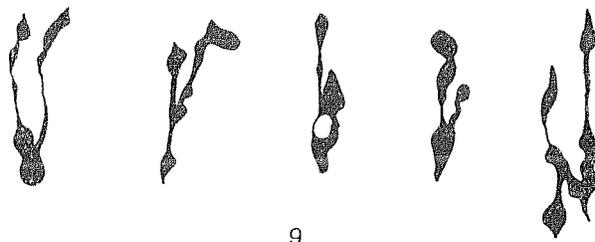
Text-fig. 9. Side-views of four trivalents and one quadrivalent from the first meiotic division of the hybrid (× 3500). From left to right: *D-S-D*, *D-D-S*, *D-S-S*, *S-S-D*, *D-S-S-D*.

TABLE III.

The average chiasma frequency per bivalent in G. Davidsonii, G. Sturtii, *and their hybrid.*

	Mean	Standard error	Extremes	Standard deviation
G. Davidsonii				
130 bivalents at metaphase	1·75	0·04	1–2	0·43
G. Sturtii				
65 bivalents at diplotene	1·78	0·05	1–3	0·37
130 bivalents at metaphase	1·72	0·04	1–2	0·46
G. Davidsonii × G. Sturtii				
154 bivalents at metaphase formed by allosyndesis	1·06	0·03	1–2	0·37
12 bivalents at metaphase containing two chromosomes from *G. Davidsonii*	1·08	0·08	1–2	0·28
11 bivalents at metaphase containing two chromosomes from *G. Sturtii*	1·55	0·15	1–2	0·50

(Table II). The totals show that the number of univalents is the same from both parents, and that about 90 per cent. of the bivalents are formed by allosyndesis, while only about 10 per cent. are formed by autosyndesis, which latter seems to be of equal frequency between the *Davidsonii* and the *Sturtii* chromosomes. Only a few trisomes and a single quadrivalent have been observed (Text-fig. 9 and Plate XVI, fig. 5). Secondary pairing, however, is frequent, especially between the univalent chromosomes.

The chiasma frequencies have been determined from the pure species

and the hybrid (Table III). The only difference of any real significance lies between the hybrid and the pure species.

Both the anaphase of the first meiotic division and the second meiotic division show a number of those irregularities by which species hybrids with incomplete chromosome conjugation are characterised. Most of the pollen grains are empty, a fact in keeping with the sterility of the hybrid.

IV. GENERAL DISCUSSION.

Despite the large number of cytological studies of species hybrids during the last ten years, very little information is yet available on the problem of auto- and allosyndesis. It is generally presumed that the chromosome conjugation is allosyndetic in most hybrids where only bivalents have been observed, but as a rule little or no evidence is adduced in support of this view. In a few instances evidence has been obtained proving that a certain amount of autosyndesis must have taken place. For instance, in hybrids derived from parents with widely different chromosome numbers the number of bivalents has been found to be greater than the chromosome number of one of the parents (cf. Darlington, 1932 *b*).

Only occasionally has the morphology of the chromosomes enabled a distinction to be drawn between allo- and autosyndesis. Thus Meurman (1928) and Avery (1930) concluded that the conjugation was allosyndetic in some of the hybrids studied by them, namely, those belonging respectively to the genera *Ribes* and *Crepis*; Berg (1931) maintains that the conjugation is autosyndetic in the *Aegilops-Secale* hybrid, a conclusion which has been criticised on the grounds that no difference exists between the paternal and the maternal chromosomes (Darlington, 1932 *b*; Kihara and Lilienfeld, 1932). Apart from the references quoted above, the writer is not aware of more recent studies wherein the morphology of the chromosomes has indicated that both auto- and allosyndesis has taken place in the same species hybrid. For this reason, the present hybrid is of considerable interest.

All the chromosomes of each of the pure species are of approximately the same size. On the other hand, both in the somatic and the meiotic divisions the difference between the chromosome sizes of the two species has been demonstrated. This difference is also apparent in the somatic and the meiotic divisions of the hybrid. Conjugation of the chromosomes in the hybrid occurs not only between the small and the large chromosomes, but also between the small ones and between the large ones. A statistical study shows that the frequency of the univalents is the

same amongst the small and the large chromosomes, but that allosyndesis occurs about nine times more often than autosyndesis. The largest number of allosyndetic bivalents found in any pollen mother cell is ten, while both the *Davidsonii* and the *Sturtii* chromosomes show a maximum number of two autosyndetic bivalents in any one pollen mother cell. Only about half the pollen mother cells show autosyndesis, whereas all show allosyndesis. The two parental species—natives of different continents—have both $n = 13$, and are both wild types. This instance shows that one must be guarded in drawing conclusions from the chromosome conjugation in a hybrid even when both parents have the same, and a fairly low, chromosome number.

Despite the difference in the sizes of the chromosomes, both species have approximately the same chiasma frequency (Table III). There is probably a slight decrease in the chiasma frequency in *Gossypium Sturtii* from diplotene to metaphase, although the values obtained possess no mathematical significance. In most organisms examined, it appears that the chiasma frequency is more or less proportional to the size of the chromosomes (Darlington, 1932 *b*). On the other hand, the chiasma frequency in the hybrid is significantly smaller than in the pure species, especially in the bivalents formed of a *Davidsonii* and a *Sturtii* chromosome. The values obtained from the bivalents formed from autosyndesis are, however, based on numbers which are too small to justify comparison.

Since the difference in chromosome size observed in the parents is maintained in the hybrid, the inference may be drawn that chromosome size is not, in this case, determined by a genetic factor. Again, since the chiasma frequency is the same in the two wild species, it seems reasonable to suppose that the number of pairing blocks is the same. It is therefore difficult to explain the difference in sizes of the chromosomes between the two species on the same lines as in *Crepis*, "inversion, translocation, deletion, duplication, union, and fragmentation" (Avery, 1930). All such processes seem likely to change the number of pairing blocks, and therewith the chiasma frequency. The difference is most probably due to some "accessory substances" (Darlington, 1932 *a*), the nature of which is as yet unknown, as is the case with *Aesculus carnea* (Skovsted, 1929).

When one takes into consideration (1) that the parental chromosomes are of different sizes, (2) that the species are completely separated geographically, and (3) that the length of time since the separation in any species from the ancestral types must be considerable, the strong homology observed in the chromosomes in the hybrid must be regarded as remarkable.

The observations on the homology of the small and large chromosomes are in sharp contrast to those on the dissimilarity in the two sets of chromosomes in New World cottons (Skovsted, 1934). *Gossypium Davidsonii* and *G. Sturtii* are undoubtedly distantly related to most of the other species of the genus including the New World cottons. Thus *G. Davidsonii* is only known to give a viable hybrid with *G. Sturtii*, while hybridisations with other species of the genus have so far either given empty seeds (unpublished work), or plants which died in the cotyledon stage (Harland, 1928; Harland and Atteck, 1931). *G. Sturtii* is evidently more closely related to the other species of the genus since it gives viable hybrids with both Old World cottons (unpublished work), and New World cottons (Harland, 1929).

V. Summary.

1. *Gossypium Davidsonii* ($n=13$), a wild species from California, has smaller chromosomes than *G. Sturtii* ($n=13$), a wild species from Australia. This difference in chromosome size is maintained in the hybrid, and enables a distinction between the paternal and the maternal chromosomes to be made.

2. The chromosome pairing in the hybrid is incomplete, but allosyndesis takes place about nine times more often than autosyndesis. Univalents are just as frequent between the small chromosomes from *G. Davidsonii*, as between the larger chromosomes from *G. Sturtii*.

3. The chiasma frequency is the same in the pure species despite the difference in chromosome size. Contrasted with the pure species, the chiasma frequency in the hybrid is significantly smaller in the bivalents containing a *Davidsonii* and a *Sturtii* chromosome.

4. The difference in the size of the chromosomes of the species under observation is in all probability neither the result of genetic factors, nor associated with a difference in pairing blocks.

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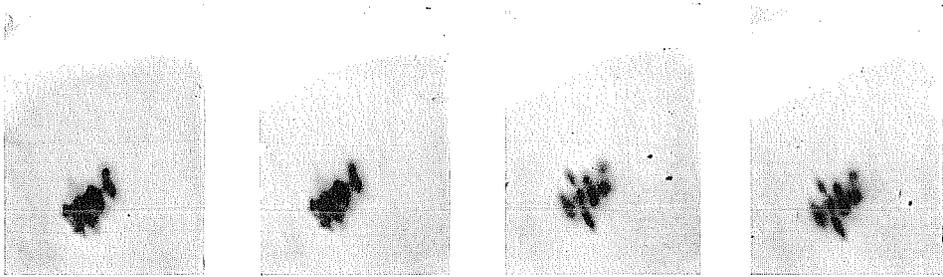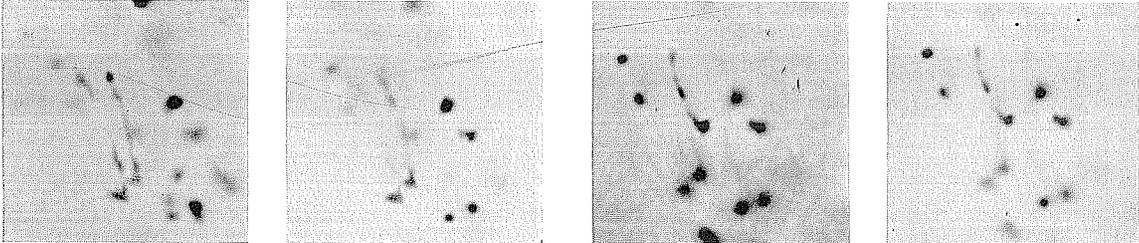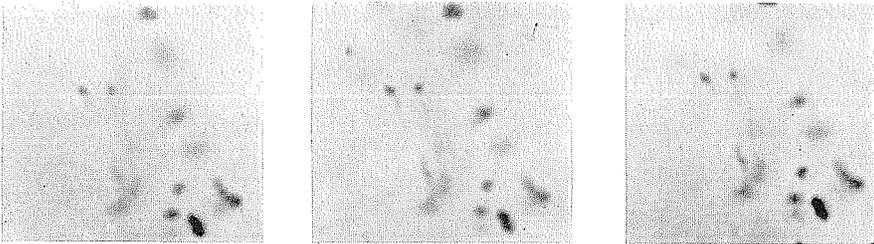Harland, S. C. (1928). "Cotton notes." *Trop. Agriculture*, Trin., **5**. 200–1.
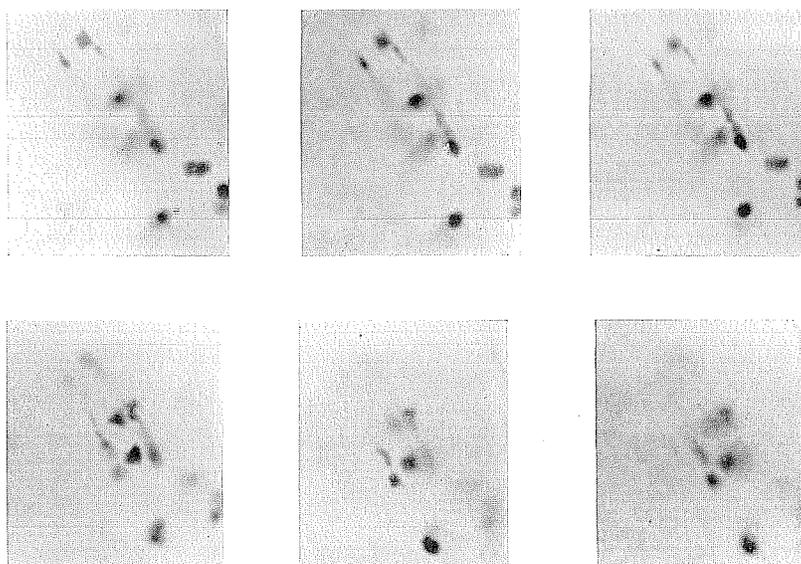
Fig. 1.

Fig. 2.

Fig. 3.

PLATE XVI

Fig. 4.

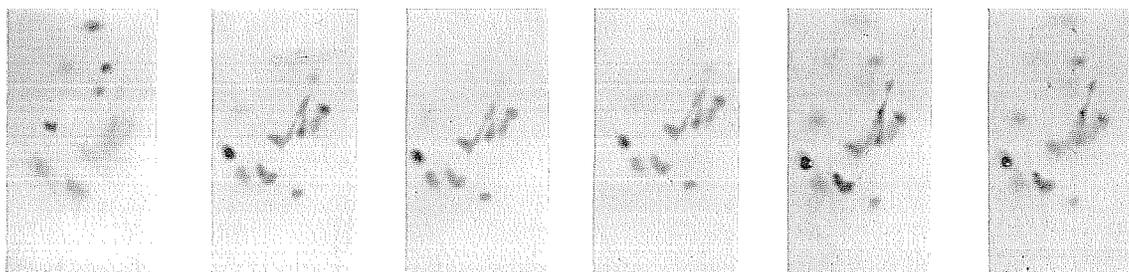Fig. 5.

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EXPLANATION OF PLATE XVI.

Figs. 1–5. Chromosomes seen in side view at metaphase of the first meiotic divisions in *Gossypium Davidsonii*, *G. Sturtii*, and their hybrid. Photographs × *circa* 2000.

Fig. 1. *G. Davidsonii* with small chromosomes.

Fig. 2. *G. Sturtii* with larger chromosomes.

Fig. 3. The hybrid with three bivalents formed of a small and a larger chromosome.

Fig. 4. The hybrid with two bivalents: one formed by allosyndesis between a small and a larger chromosome, while the other bivalent is autosyndetic and contains two larger (*i.e. Sturtii*) chromosomes.

Fig. 5. A trivalent from the hybrid formed of two small and one larger chromosomes.