INVERSIONS IN *FRITILLARIA*

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(With Plate XV, Forty-Six Text-figures and One Diagram)

Introduction

Cytological observations on hybrids have revealed inversion as an important mechanism in distinguishing related species (Müntzing, 1934; Richardson, 1936; Upcott, 1937). The occurrence of inversions, however, is not confined to species hybrids or to derivatives from X-ray treatment (McClintock, 1931, 1933). They have been found in species of wild grasshoppers (Darlington, 1936*b*) and of asexually propagated plants (Smith, 1935; Richardson, 1936; Upcott, 1937; Doughty, 1936). Dr Darlington's collection of slides comprising nearly thirty species of *Fritillaria*, which was kindly made available for this investigation, encouraged a systematic search for evidence of inversions in this genus, particularly since structural hybridity due to translocations had been inferred in several species (Darlington, 1936*a*).

Methods of fixation have been described previously (Darlington, 1936*a*). All preparations were made by Mr L. La Cour. Illustrations were made at bench level with a camera lucida at a magnification of 3300 and reduced to 1100, except in Text-figs. 40–46, which were made at 1650 and reduced to 550.

I am indebted to Mr L. La Cour and to Mr H. C. Osterstock for the photographs.

Occurrence of chromatid bridges

For most of the species listed below material available allowed reliable conclusions on the presence or absence of chromatid bridges at meiosis and on the frequency of their occurrence. In general, at least one hundred cells between anaphase I and telophase II have been studied. An asterisk in the following list indicates a scarcity of material.

No chromatid bridges were found in the following species

F. imperialis	*F. obliqua*
F. Meleagris	*F. recurva* 2*x*
F. pallidiflora	*F. oranensis*
F. acmopetala	*F. gracilis*
F. pontica	*F. hispanica*
F. Elwesii	*F. latifolia* 2*x*
*F. pluriflora**	*F. latifolia* 3*x*
F. Eggeri	*F. karadaghensis*
F. verticillata	*F. meleagroides*
F. Thunbergii	*F. lanceolata*
F. phenanthera	*F. ruthenica*[1]

Chromatid bridges were found in the following species

F. pudica 3*x*	*F. dasyphylla* 3*x*
F. citrina 2*x*	*F. recurva* 3*x*
F. dasyphylla 2*x*	

Inversions in *Fritillaria dasyphylla* 2*x*

F. dasyphylla, like many other species of *Fritillaria* (Darlington, 1936*a*) and *Lilium* (Richardson, 1936), has two pairs of chromosomes with submedian centromeres (*M*) and ten pairs with subterminal centromeres (*S*) (Text-fig. 1).

In meiosis, pairing as a rule is normal for the large majority of the bivalents. The mean chiasma frequency of 3·5 per bivalent is similar to that of other species of *Fritillaria* with free chiasmata. Disjunction in anaphase I is also normal, with the exception of a very high frequency of one and rarely two "chromatid bridges" per nucleus (Pl. XV, fig. 1). No univalents have been seen in the hundreds of cells studied, at anaphase or at metaphase.

Richardson (1936) has analysed the expected consequences of crossing-over in structurally differentiated bivalents. It is evident that the anaphase behaviour of bivalents possessing an inverted segment facilitates a direct cytological determination of the interrelations of successive chiasmata where crossing-over is high in the inversion or both in the inverted and in the proximal regions.

The evidence which shows that inversions may be responsible for the chromatid bridges in *F. dasyphylla* is similar to that obtaining for the hybrid *Lilium Martagon* × *L. Hansonii* (Richardson, 1936);

[1] Inversions have since been found in another form of *F. ruthenica*. C. D. Darlington.

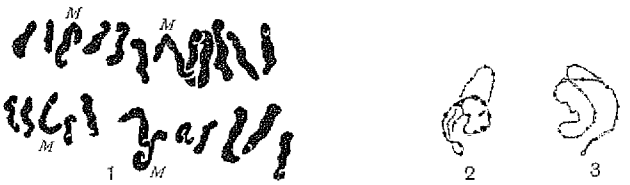
(*a*) Inversion loops have been observed in pachytene (Text-figs. 2 and 3).

(*b*) Wherever accurate observation has been possible, the chromatids of the bivalents concerned, apart from the bridge, showed symmetrical distribution (Text-figs. 4–7).

(*c*) Acentric fragments, associated with a loop chromatid in one daughter complement at anaphase I, as well as second division bridges occur (Text-figs. 9–11). Their frequencies are of comparable magnitude (Table I *C*).

It is therefore concluded that the chromatid bridges in *Fritillaria dasyphylla* are due to crossing-over in one or more inversions which do not include the centromere.

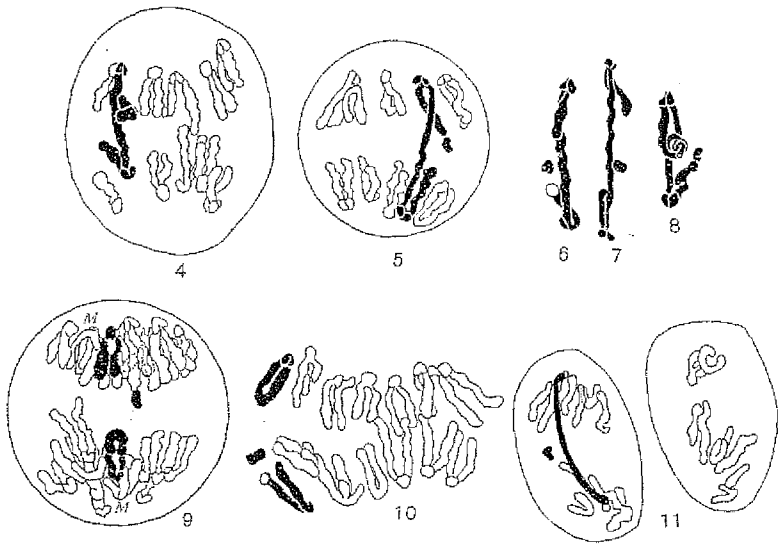
The following evidence is adduced to show that the majority of chromatid bridges are caused by one terminal or nearly terminal inversion in the long arm of one *S*-chromosome, whilst a small number are caused by a subterminal inversion in the long arm of another, possibly shorter, *S*-chromosome:



Text-fig. 1. *F. dasyphylla* 2*x*. Anaphase II. 2*M* and 10*S* chromosomes (unmarked).
Text-figs. 2, 3. *F. dasyphylla* 2*x*. Pachytene loop.

(*a*) One dicentric chromatid in an *S* bivalent is found associated with one short acentric fragment in the preponderant number of cells with chromatid bridges (Text-figs. 3–6). The lengths of chromatid arms in comparable cells show good correspondence. The acentric fragment without a dicentric chromatid which is frequently seen in anaphase I is of a length similar to that of the fragment associated with the chromatid bridges referred to above. The nearly terminal position of the pachytene loops (Text-figs. 2 and 3), the high frequency of crossing-over in the inversion (see Table I), the occurrence of double chromatid bridges (Text-figs. 16–19), and, perhaps, of two second-division bridges (Text-fig. 20), and the absence of evidence of crossing-over distal to the inversion, indicate that the inversion is terminal or closely terminal and that therefore the inverted region is as large, or nearly as large, as the fragment, that is, about one-third of the size of the long arm of the bivalent.

(*b*) Amongst the many hundreds of cells studied at anaphase and telophase I and interphase, not one has been observed exhibiting two



Text-figs. 4–8. *F. dasyphylla* 2*x*. Anaphase I. Chromatid bridge with "short" fragment (inversion *A*).
Text-figs. 9, 10. *F. dasyphylla* 2*x*. Loop chromatid with "short" fragment.
Text-fig. 11. *F. dasyphylla* 2*x*. Anaphase II, second-division bridge.

TABLE I

Frequencies per pollen mother cell of anaphase configurations in the bivalent carrying Inversion A

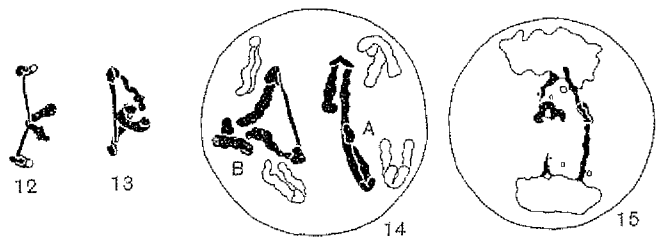
		First-division			Second-division		
		Configuration	Absolute	Percentage	Absolute	Percentage	Configuration
	A	$B_1^{I}+f_1$	52	47·7	59	41·2	$B_1^{I}+f_1$
	B	$B_2^{I}+f_2$	2	1·8	—	—	$B_2^{I}+f_1$
	C	No B, f_1	21	19·2	33	23·1	$B_1^{II}+f_1$
	D	No B, f_2	—	—	1	0·7	$B_2^{I}+f_2$
	E	—	—	—	3*	2·1*	No B, f_1
Total	*A–E*			68·7		67·1	
	F	No B nor f	34	31·3	47	32·9	No B nor f
			109	100·0	143	100·0	

* Presumably to be added to $B_1^{I}+f_1$.

(separate) chromatid bridges with two short fragments. Since, on the other hand, the rarely crossing-over Inversion *B* (see below) has in three instances been seen in combination with the short fragment inversion, it is concluded that one single inversion is responsible for all, or nearly all,

chromatid bridges with a short fragment. This inversion will henceforth be called "Inversion *A*".

(*c*) A small number of chromatid bridges with a characteristically larger acentric fragment have been observed (Text-figs. 12–15). Since the width of the chromatid bridge is inversely correlated with the size of the fragment (Richardson, 1936), the dicentric chromatid is distinctly narrower and at corresponding stages shorter than that of Inversion *A* (Text-fig. 14). In consequence it tends to break more easily in interphase (Text-fig. 15). The low frequency of chiasma formation in this inversion, the absence of double bridges, and the indication of distal crossing-over (Text-fig. 14), point to a small inversion at some considerable distance from the distal end of an *S* bivalent. This inversion will be called "Inversion *B*".



Text-figs. 12, 13. *F. dasyphylla* 2*x*. Chromatid bridge with "long" fragment (Inversion *B*).
Text-fig. 14. *F. dasyphylla* 2*x*. Anaphase I, Inversions *A* and *B*.
Text-fig. 15. *F. dasyphylla* 2*x*. Interphase, Inversions *A* and *B*.

Analysis of chiasma formation in the bivalent carrying Inversion A

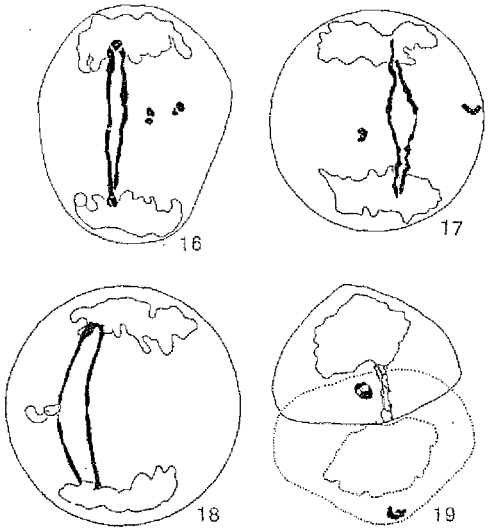
All types of disjunction to be expected in a bivalent with a terminal or nearly terminal inverted region have been found.

(1) *A dicentric chromatid and an acentric fragment* (Text-figs. 4–8). In morphology and behaviour this configuration is similar to those described in *Lilium* (Richardson, 1936). The behaviour between telophase I and the tetrad stage shows a large amount of variation (Text-figs. 21–28). The bridge frequently shows a point of weakness about the centre (Text-fig. 21). It may break there or at some other place, presumably owing to the formation of the cell wall across the bridge (Text-figs. 22–23). It may, however, remain intact to the second telophase (Text-figs. 24 and 27). The uncoiling is also subject to wide variations (Text-figs. 22 and 23).

(2) *An acentric fragment at anaphase I, with a loop chromatid in one of the daughter halves* (Text-figs. 9 and 10). This configuration gives rise to a chromatid bridge in the second anaphase (Text-fig. 11). The loop

chromatid associated with a fragment has been seen in many instances. In Text-fig. 9 the position of the proximal chiasma can still be seen. Correspondence of these configurations in both divisions is satisfactory (Table I*C*).

(3) *Two chromatid bridges in the same bivalent with two short fragments* (Text-figs. 16–19 and Pl. XV, figs. 2 and 3) have been seen in few cells. This



Text-figs. 16–18. *F. dasyphylla* 2*x*. Telophase I. Double chromatid bridge.
Text-fig. 19. *F. dasyphylla* 2*x*. Interphase. Probably double chromatid bridge.

Text-fig. 20. *F. dasyphylla* 2*x*. Telophase II. Two second-division bridges, presumably arising from two complementary chiasmata in the inversion, disparate to one proximal chiasma.

configuration is due to two complementary chiasmata in the inversion. A similar configuration has been described by Smith (1935) in *Trillium erectum* (once in many hundreds of cells), by Richardson (1936) in *Lilium umbellatum* var. *erectum*, and, probably, by Müntzing (1934, Fig. 24) in *Crepis divaricata* × *dioscoridis*.

(4) *Two bridges in the second division, with two acentric fragments,* are due to two complementary chiasmata in the inversion disparate to a

third proximal to the inversion (Darlington, 1936*a*). Text-fig. 20 presumably illustrates this configuration. It is unlikely that the two bridges in telophase II are due to Inversions *A* and *B*, since the latter forms a narrow bridge which breaks at an early stage. Two inversions, with short fragments which might give rise to this configuration, have not been seen in any other cell (see above).

TABLE II

Expected consequences of one or two chiasmata in the inversion with 0, 1 *or* 2 *chiasmata proximal to the inversion*

A. One chiasma in inversion

	Proximal chiasmata	B_0	B_1^{I}	B_2^{I}	B_1^{II}	B_2^{II}
(*a*)	0	—	×	—	—	—
(*b*)	1 : comparate	—	×	—	—	—
(*c*)	disparate	—	—	—	×	—
(*d*)	2 : 1 comparate + 1 comparate	—	×	—	—	—
(*e*)	1 disparate + 1 comparate	—	—	—	×	—
(*f*)	1 comparate + 1 disparate	—	×	—	—	—
(*g*)	1 disparate + 1 disparate	—	×	—	—	—

B. Two chiasmata in inversion

	Proximal chiasmata	Chiasmata in inversion					
(*h*)	0	2 reciprocal	×	—	—	—	—
(*i*)	1 comparate	2 reciprocal	×	—	—	—	—
(*j*)	1 disparate	2 reciprocal	×	—	—	—	—
(*k*)	0	2 complementary	—	—	×	—	—
(*l*)	1 complementary—disparate	2 complementary	—	—	×	—	—
(*m*)	1 complementary—reciprocal	2 complementary	—	—	×	—	—
(*n*)	1 disparate—disparate	2 complementary	—	—	—	—	×
(*o*)	0	2 disparate	—	×	—	—	—
(*p*)	1 disparate—comparate	2 disparate	—	—	—	×	—

The frequencies of the various anaphase configurations (Table I) were determined in anaphase I and II respectively; in both divisions frequencies are given per p.m.c. Their interpretation in terms of chiasma formation can be approached only with a knowledge of the chiasma frequency at metaphase. Since it is not possible to identify at metaphase the bivalent which carries Inversion *A*, the chiasma frequencies have been determined in the long arm of all *S* bivalents (Table III).

TABLE III

Chiasma frequency at metaphase in the long arm of S *bivalents*

No. of nuclei	No. of bivalents	No. of bivalents with different nos. of chiasmata					Total number of chiasmata	Chiasmata per bivalent
		0	1	2	3	4		
6	60	0	0	20	25	15	175	2·9

In not one among the many cells inspected has an *S* bivalent been observed with a single chiasma in the distal region. Hence the possibility of one chiasma in the inverted region, without any proximal chiasmata (Table II (*a*)), can be excluded. The expected consequences of one chiasma proximal to the inversion have been explored by Richardson (1936). They are quoted in Table II (*b*)–(*c*). Diagram 1 and Table II (*d*)–(*g*) illustrate the expectation on the formation of two proximal chiasmata.

The formation of chromatid bridges in anaphase is modified by chiasmata proximal to the inversion in the following manner:

(1) Any number of comparate (i.e. reciprocal and complementary) chiasmata proximal to one chiasma in the inversion give a first-division bridge.

(2) One (proximal) disparate chiasma, irrespective of the number of comparate chiasmata formed distal to it, will cause the formation of a second-division bridge.

(3) Any chiasma formed proximal to the disparate chiasma referred to under (2) causes the formation of a first-division bridge, i.e. "cancels out" the second-division bridge.

(4) One further proximal comparate, or two further proximal disparate chiasmata, however, restore the second-division bridge.

It remains to discuss the expectation on the formation of two chiasmata in the inversion, with or without the formation of proximal chiasmata (Table II (*h*)–(*p*)). The effect of several proximal chiasmata can be determined by applying the principles set out above. From the bivalent configurations in metaphase it can be concluded that two chiasmata in the inversion are in more than half the cells associated with one or more proximal chiasmata.

Two reciprocal chiasmata in the inversion, irrespective of the formation of proximal chiasmata, form no bridge, thus being indistinguishable from the absence of chiasmata in the inversion altogether. Two disparate chiasmata give one bridge either in the first or in the second division, depending on the chiasma formation in the proximal region. Two complementary chiasmata give rise to two bridges from one bivalent, a double chromatid bridge at the first division, or one bridge in each cell at the second. The latter configuration arises from one proximal chiasma disparate in relation to both chiasmata in the inversion, or from any other proximal chiasma, combined with a disparate second proximal chiasma. Thence it is possible to estimate directly the proportion of bivalents forming two complementary chiasmata in the inversion.

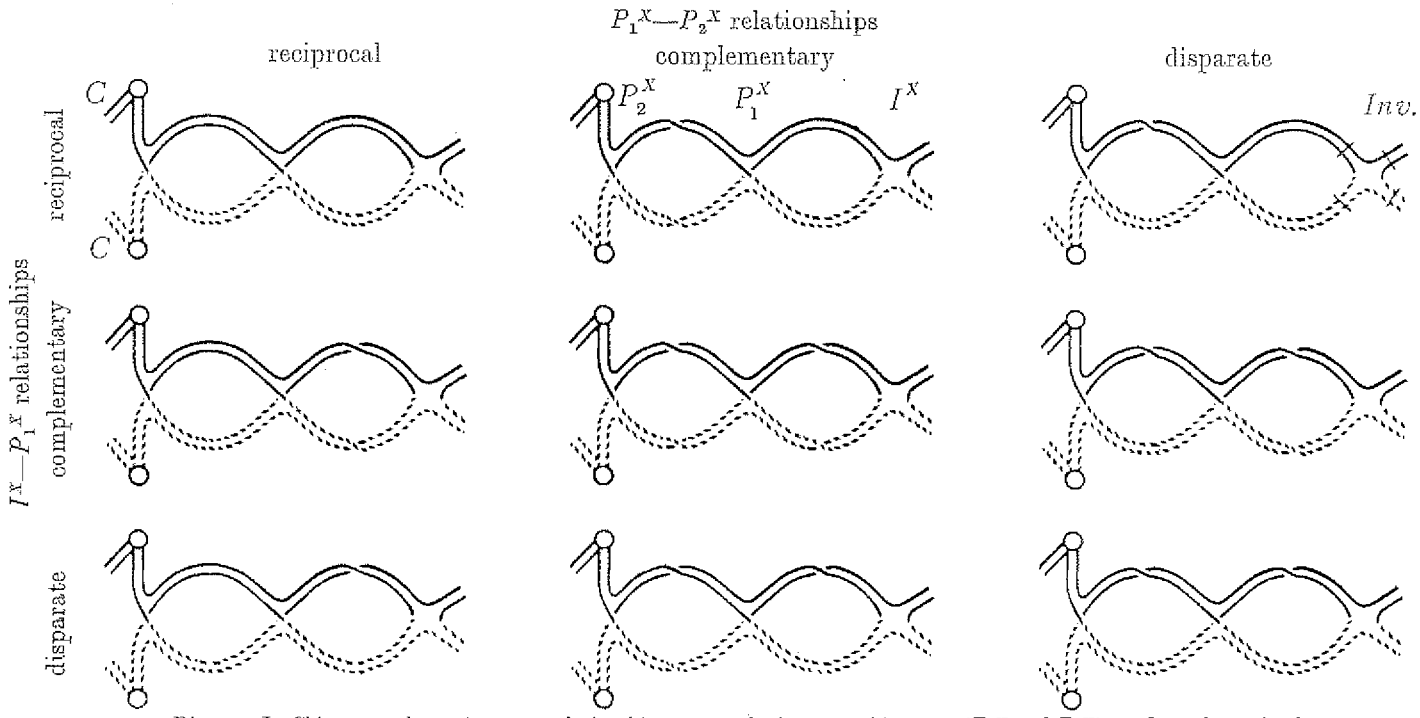
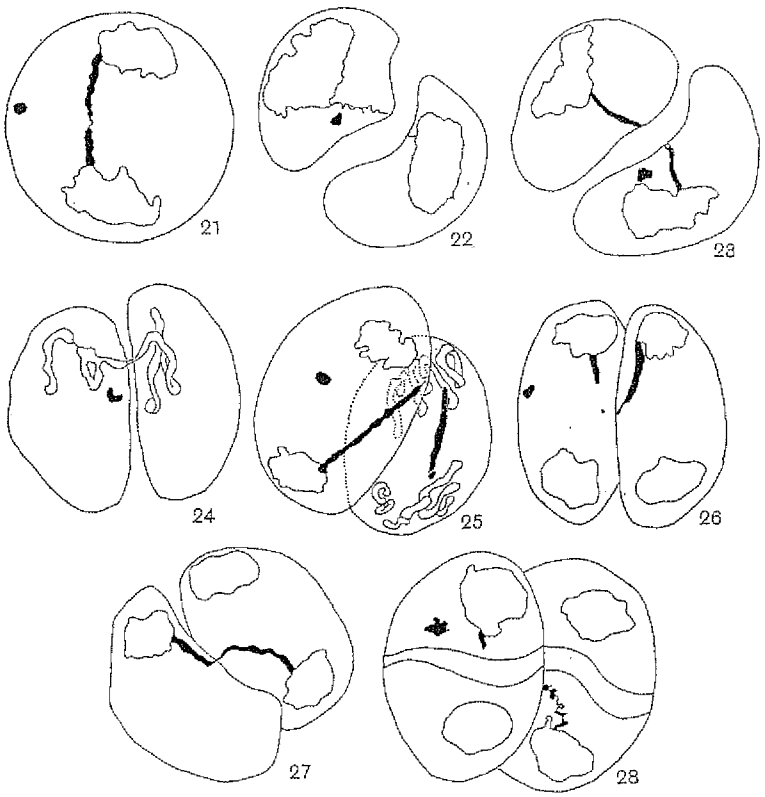


Diagram I. Chiasma and crossing-over relationships expected when two chiasmata (P_1X and P_2X) are formed proximal to a chiasma in an inverted segment (limits marked under *Inv.*). Centromeres, *C*.

Applying these expectations to the frequencies listed in Table I, the following conclusion can be drawn for the bivalent carrying Inversion *A*:

(1) Double crossing-over in the inversion is rare. Two complementary chiasmata have a frequency of about 2·5 per cent (Table I*B* and *D*).

(2) About 33–34 per cent of cells contain no bridge. Hence 30–31 per cent form no chiasma in inversion *A* assuming that the frequency of two



Text-figs. 21–23. *F. dasyphylla* 2*x*. Interphase.
Text-figs. 24–27. *F. dasyphylla* 2*x*. Telophase II.
Text-fig. 28. *F. dasyphylla* 2*x*. Tetrad.

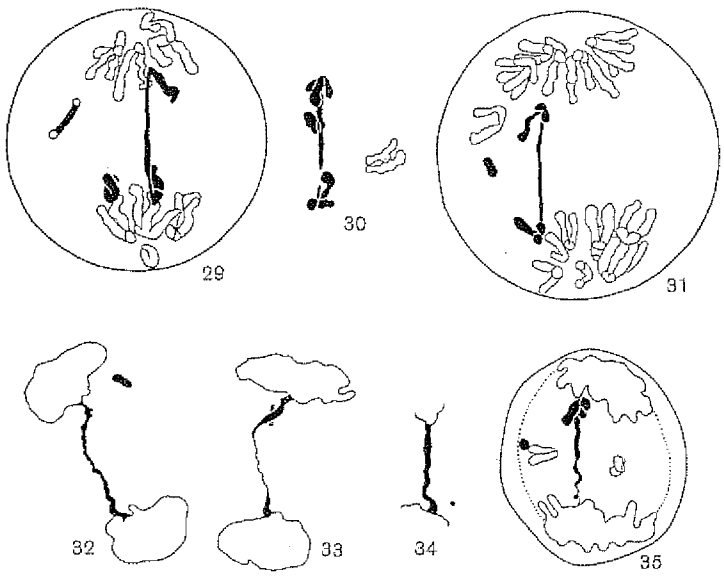
reciprocal chiasmata in the inversion (Table II (*h*)–(*j*)) is similar to that of two complementary chiasmata (see (1)) (Table I*F*).

(3) Two disparate chiasmata in the inversion (Table II (*o*)–(*p*)) presumably amount to no more than about 5 per cent, i.e. twice the frequency of two complementary chiasmata. Thus, since the total number of single bridges in first and second division is 65 per cent (Table I*A* and *C*) and since at least two and not more than four chiasmata

are formed in the long arm of S bivalents at metaphase, the bivalent carrying Inversion A forms one chiasma in the inversion and from one to three chiasmata proximal to it in about 60 per cent of cells. Of this amount the number of first-division bridges (about 40 per cent) is twice as large as that of second-division bridges (about 20 per cent). This can be explained at least partially by the fact that a second disparate chiasma proximal to a (first) disparate chiasma "cancels out" the second-division bridge (Table II (g)), and that similar relations obtain also for three proximal chiasmata. It is doubtful whether this fully explains the preponderance of first-division bridges, so that there is an indication of a preponderance of comparate over disparate chiasmata.

Inversions in F. dasyphylla 3x, F. pudica 3x, F. recurva 3x *and* F. citrina

In *F. dasyphylla*, a small number of chromatid bridges were found at anaphase I. Owing to the presence of univalents, dicentric chromatids



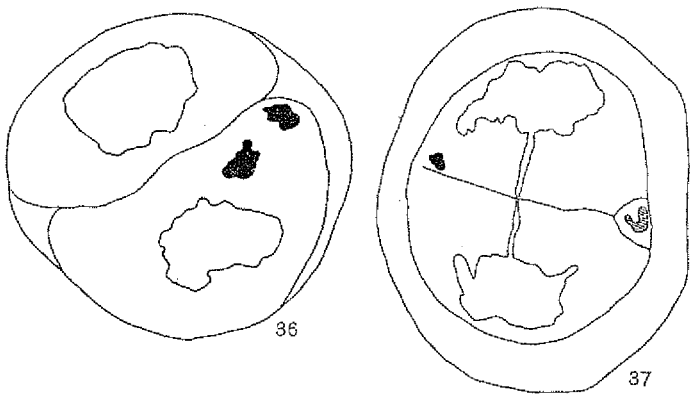
Text-figs. 29–31. *F. dasyphylla* 3x. Anaphase I.
Text-figs. 32, 33. *F. citrina*. Interphase.
Text-figs. 34, 35. *F. pudica* 3x. Telophase I and interphase.

only have been counted. Their frequency is 3·4 per cent. In type they mostly resemble Inversion A of the diploid form of the same species (Text-figs. 29–30), but one was found resembling Inversion B (Text-fig. 28).

In *F. pudica* three bridges were found in forty-three cells (Text-figs. 34 and 35). They are associated with short fragments. The frequency in *F. citrina* is considerably lower: only two bridges were found in 150 cells (Text-figs. 32 and 33). Two bridges were seen in *F. recurva* 3*x*.

Cell-wall formation in *Fritillaria dasyphylla*

Univalents or fragments, lagging in the first or second meiotic divisions, are usually excluded from the daughter nuclei, either lying in the plasma of one of these (micronuclei), or forming separate cells (microcytes).[1] They have been frequently described in triploid hybrids and species (e.g. cf. Darlington, 1929). The formation of a separate cell



Text-fig. 36. *F. dasyphylla* 3*x*. Interphase. Micronuclei.
Text-fig. 37. *F. dasyphylla* 3*x*. Telophase I. Microcyte, bridge and fragment.

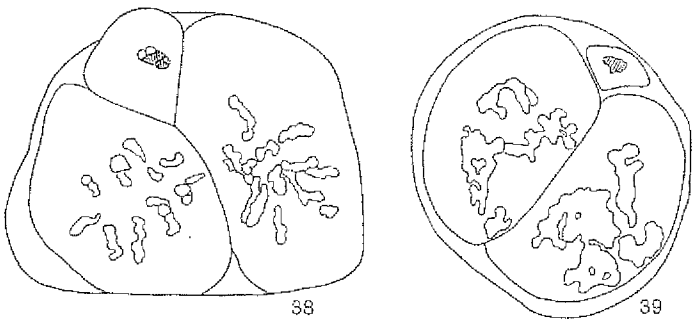
wall may be due to the chance position of the univalent or fragment in relation to the daughter nuclei, to the reaction between its centromere (missing in acentric fragments) and the poles (Darlington, 1936*a*), to its relative size, or to a combination of several of these elements.

The frequent occurrence of both lagging univalents and acentric fragments in *F. dasyphylla* facilitates the analysis of cell-wall formation in microspores. In the triploid, they occur side by side; but since chiasmata in the inversion are rare, and further since bridges can as a rule be recognized as far as the tetrad stage, there is little danger of confounding centric and acentric units (Text-fig. 37). In the diploid, on the other hand, univalents have never been seen, either at metaphase or at anaphase. All fragments therefore can be assumed to be acentric.

[1] In the text-figures the former are drawn in black, the latter barred.

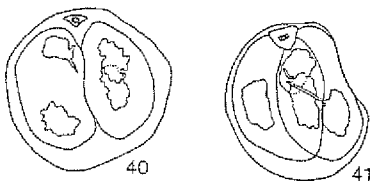
F. dasyphylla 3*x*

When a cell wall is formed at telophase I, the majority of lagging univalents are included in one of the daughter cells. A separate cell wall—with a frequency of about 9 per cent at interphase—is formed only when a univalent is situated in the dividing plane between the daughter cells



Text-fig. 38. *F. dasyphylla* 3*x*. Metaphase II. Microcyte.
Text-fig. 39. *F. dasyphylla* 2*x*. Metaphase II. Microcyte.

close to the periphery. The microcyte receives a wedge-like form (Text-figs. 37 and 38). Differentiation is sharply defined: univalents lying in closest proximity to the newly formed cell wall, but not in its plane, are always included (Text-fig. 36). In several instances a microcyte was observed containing one half of a divided univalent, whilst the other half, connected to it, but lying off the equator of the cell, was excluded from the microcyte.

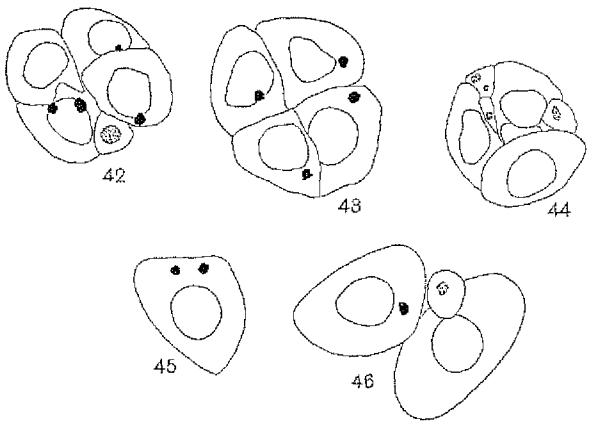


Text-figs. 40, 41. *F. dasyphylla* 2*x*. Telophase II.

In the second division the mechanism of cell-wall formation is similar. Only units lying in one of the dividing planes receive separate cell walls. Thus some tetrads contain both micronuclei and microcytes, others only the one or the other (Text-figs. 42–44). Up to six units have been observed in one tetrad cell. The pollen grains contain from 0 to 3 micronuclei (Text-fig. 45). A microcyte is illustrated in Text-fig. 46, with a nucleus no larger than the neighbouring micronucleus presumably derived from the same tetrad cell.

F. dasyphylla 2*x*

In the diploid, micronuclei are due to the presence of acentric fragments. Their frequency accordingly is much lower than in the triploid. At interphase, metaphase II and telophase II, microcytes have been



Text-fig. 42. *F. dasyphylla* 3*x*. Tetrad with microcyte and micronuclei.
Text-fig. 43. *F. dasyphylla* 3*x*. Tetrad with micronuclei only.
Text-fig. 44. *F. dasyphylla* 3*x*. Tetrad with microcytes only.
Text-fig. 45. *F. dasyphylla* 3*x*. Pollen grain with micronuclei.
Text-fig. 46. *F. dasyphylla* 3*x*. Pollen grains and microcyte.

observed in several instances (Text-figs. 39–41). Tetrad material was insufficient for accurate observation. The mechanism of cell-wall formation is analogous to that described for the triploid: only units in the dividing planes receive a separate cell wall.

Discussion

In view of the fact that acentric fragments may give rise to the formation of separate cells, it cannot be maintained that the presence of a centromere is a necessary requirement for cell-wall formation. The evidence for cell-wall formation by acentric fragments as well as by univalents suggests that it is chiefly or entirely the position of the lagging unit in the cell which determines the formation of a separate cell wall. Unless it ranges in the equator of the cell, i.e. in a position of balance relative to the major nuclear units, it fails to form an independent cell wall. Furthermore, it is only those fragments or univalents attaining the maximum distance from the daughter nuclei which form microcytes. It may be concluded that only the maximum satisfaction of repulsion between nuclear units secures the formation of a cell wall.

SUMMARY

1. In twenty-two species of *Fritillaria* no evidence of inversions has been found.

2. In the following species, viz. *F. dasyphylla* $2x$, *F. dasyphylla* $3x$, *F. pudica* $3x$, *F. citrina* and *F. recurva* $3x$, the results of crossing-over in inversions have been observed.

3. Inversion *A* in *F. dasyphylla* $2x$, located at, or near, the distal end of an *S* bivalent, has a frequency of about 70 per cent of one or two chiasmata in the inversion.

4. The expected configurations for more than one chiasma proximal to the inversion are analysed.

5. Chiasma formation in the bivalent carrying inversion *A* has been studied. The frequencies of the various configurations indicate a slight preponderance of comparate chiasmata.

6. Cell-wall formation by acentric fragments and univalents has been studied in *F. dasyphylla*. The formation of a separate cell wall requires a position of the lagging unit satisfying the maximum repulsion from both daughter nuclei. The possession of a centromere by the micronucleus is not apparently indispensable.

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EXPLANATION OF PLATE XV

Fig. 1. *F. dasyphylla* 2*x*. Interphase.

Fig. 2. *F. dasyphylla* 2*x*. Anaphase I, double chromatid bridge. Identical with Text-fig. 16.

Fig. 3. *F. dasyphylla* 2*x*. Anaphase I, double chromatid bridge. Identical with Text-fig. 17.

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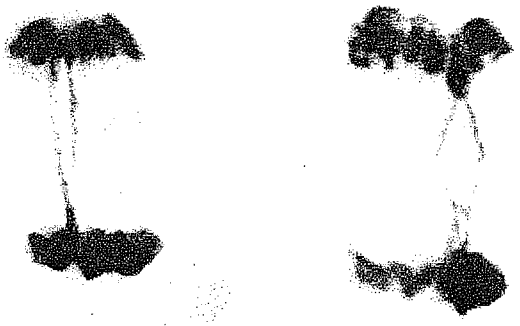

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