

# The Nature and Possible Cause of U-Type Bridge and Loop Configurations in Three Species of Trillium

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Masaaki IHARA\* : The Nature and Possible Cause  
of U-Type Bridge and Loop Configurations  
in Three Species of *Trillium*

井原正昭\* : 北米産エンレイソウ 3 種に見られた  
U—型染色分体橋及び環の特徴

Spontaneous dicentric bridges associated with fragment (s) have been regarded as crossovers resulting from paracentric inversions (McCLINTOCK 1933, 1938; BROWN and ZOHARY 1955; SJÖDIN 1971) and thus indicative of inversion heterozygotes (SMITH 1935; FRANKEL 1937; UPCOTT 1937; BRANDHAM 1969 a, 1977; GUSTERFSSON 1972; others). However, there are alternative explanations for the occurrence of spontaneous chromatid bridges which attribute crossing over at non-inverted segments, viz., U-type crossing over (MATSUURA 1950; WALTERS 1950; HAGA 1953; JOHN *et al* 1969; LEWIS and JOHN 1966; NEWMAN 1966, 1967; JONES 1968, 1969; JONES and BRUMPTON 1971; BRANDHAM 1969 b, c, 1970).

This paper describes 1) the frequency of dicentric bridges and chromatid loops in *T. grandiflorum* SALISB. ( $2n=10$ ), *T. discolor* WRAY ( $2n=10$ ) and *T. stamineum* HARBISON ( $2n=10$ ); 2) the normal meiotic development and meiotic stages affected by a temperature shock in *T. discolor* and *T. stamineum*; and 3) a hypothesis for the nature of the break and rejoining of the chromosomes.

#### Materials and Methods

*Source of materials* The plants used in this study were chosen from the population samples collected at localities listed in Table 1.

*Cultivation* The plants were cultivated in a nursery garden of the Biology Department, Vanderbilt University, Nashville, TN., U. S. A. Rhizomes with flower buds

were dug from the garden and were transferred to the laboratory for the indoor treatment: the rhizomes were either kept in a refrigerator (4°C) or soaked in a water bath filled with running water ( $9.0 \pm 0.5^\circ\text{C}$ ). The room temperature was kept at 20–25°C.

*Cytological preparation* Microsporocytes were squeezed out directly onto clean glass slides, fixed with Newcomer's fluid (NEWCOMER 1953) for 5 min, stained with 1 per cent aceto-orcein for more than 5 min and squashed gently with cover glasses. Permanent preparations were not made. Scanning observations were done at  $\times 600$  magnification and some critical figures were drawn with an Ernst Leitz camera lucida at  $\times 970$ .

*Identification of chromosomes* The nomenclature of the individual chromosomes was in accordance with the Japanese system (e. g., HAGA 1934). Meiotic stages were defined according to HUSKINS and SMITH (1935) as well as MATSUURA (1937). The half-chromatids of WILSON *et al* (1959) were not detected in any of the cells examined.

*Developmental monitoring* Periodical examination was made at 2-week intervals; in each survey a flower bud was taken from 5 different rhizomes. Outer scaly leaves of the flower buds were peeled away and the longest anther was used for cytological examination.

#### Results

*Aberrations under spontaneous and chilled conditions in T. grandiflorum*

Table 1. Original localities of the plants used for the present investigation

Species	Localities (Collection no.)
<i>T. discolor</i> WRAY	Edgefield Co., SC (#S-1131)
<i>T. grandiflorum</i> SALISB.	4.8 Km NW of Monteagle, Grandy Co., TN. (#S-1100)
<i>T. stamineum</i> HARBISON	4.2 Km S of US 100 across S. Harpeth R., Williamson Co., TN. (#I-42)

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35 flower buds of 15 rhizomes of *T. grandiflorum* were examined at the end of October. Of 35 buds, 31 contained microsporocytes in the pollen grain stage, and the remaining 4 were in various stages of microsporogenesis (Table 2). The univalent or desynaptic

configuration (Fig. 1 b) was seen in a single anther of a flower bud. The arm of the univalent chromosomes appeared to consist of paired chromatids, but the size was rather larger than that of a normal bivalent chromosome composed of 4 chromatids (Fig. 1 a). The

Table 2. Meiotic stages and length of anthers within a flower bud of *T. grandiflorum*

Plant no. Bud no.	1					2			3				4		
	I	II	III	IV	V	I	II	III	I	II	III	IV	I	II	III
1	— Pg	— Pg	— Pg	10.5 Pg	7.5 Int	— Pg	— Pg	8.0 Pg	— Pg	— Pg	— Pg	7.5 Pt	— Pg	10.0 Pg	7.0 Pc
2	—	—	—	10.3 Pg	7.2 Int-TII	—	—	8.0 Pg	—	—	—	7.5 Pt	—	—	7.0 Pc
3	—	—	—	10.3 Pg	7.2 Int-TII	—	—	7.8 Pt-Pg	—	—	—	6.5 AI-TII	—	—	7.2 MI-AI <sup>1)</sup>
4	—	—	—	9.0 Pg	6.8 Dp-AI	—	—	7.2 Pt-Pg	—	—	—	6.5 MI-AII	—	—	6.5 MI-AI <sup>2)</sup>
5	—	—	—	8.5 Pg	6.2 Dp-AI	—	—	7.0 Pt	—	—	—	6.0 Dp-Dk	—	9.5 Pg	6.0 Dk-MI <sup>3)</sup>
6	—	—	10.0 Pg	8.3 Pg	5.8 Dk-AI	—	—	7.0 MI <sup>1)</sup>	—	—	8.5 Pg	5.2 Pc <sup>2)</sup>	—	9.0 Pg	5.8 Pc-Dp <sup>3)</sup>

1) Desynaptic pairs were involved. 2) Somatic chromosome-like prophase. 3) Observed after chilling. Abbreviation: Pg (pollen grain stages), Pt (pollen tetrad stages), TII (telophase II), AII (anaphase II), Int (interphase), AI (anaphase I), MI (metaphase I), Dk (diakinesis), Dp (diplotene), Pc (pachytene) and — (not examined). Length in mm.

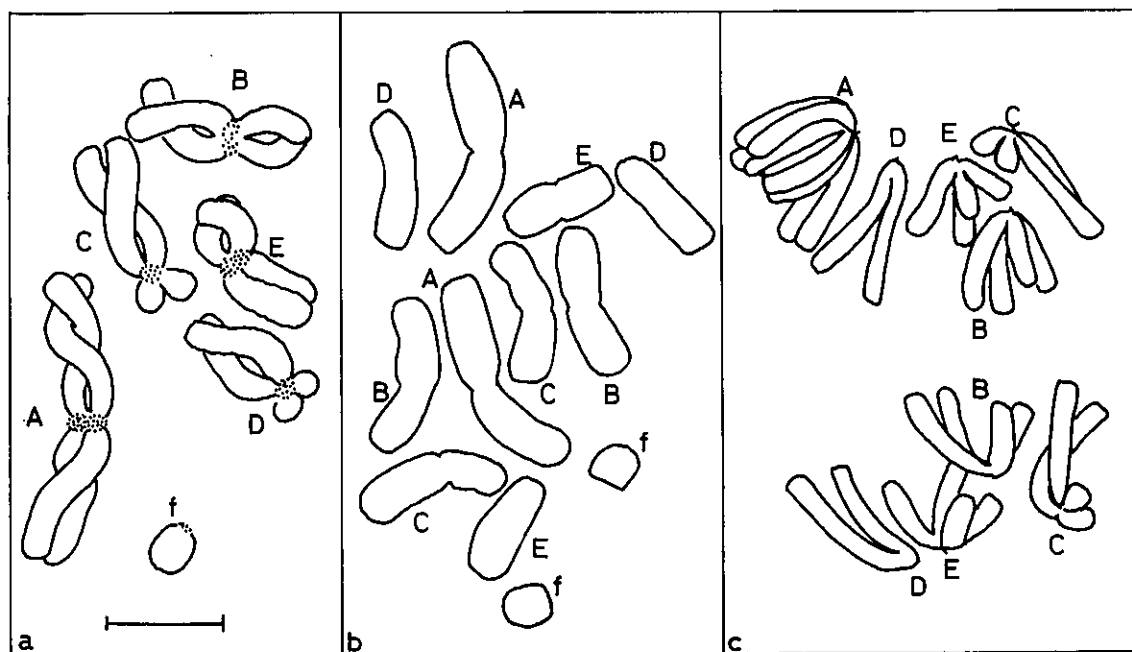


Fig. 1. Normal bivalents and spontaneous abnormal chromosomes in *T. grandiflorum*. (a) Normal 5 bivalents and one paired supernumerary chromosome. (b) Desynapsed 10 univalents and 2 supernumerary chromosomes, probably induced by environmental disturbance. (c) Normal 4 disjoined pairs and non-disjunction in chromosome A. Scale denotes 10  $\mu$ m.

situation is comparable to that described for desynaptic pairs of *T. kamschaticum* PALL. (MATSUURA 1937), in which the desynapsis was presumably the result of the flower buds being transferred into a warm greenhouse in early autumn.

Plant no. 4 of *T. grandiflorum* exhibited early prophase in the longest and the second longest anthers of the 3<sup>rd</sup> flower bud, although the other two flower buds contained meiocytes at the pollen grain stage (cf. Table 2). The flower bud was kept in a refrigerator (4°C) for 2 weeks; the remaining anthers were re-examined for their meiotic stages. Results are summarized in Table 3. Some selected figures are illustrated in Figures 1 c and 2, which may be classified into two types, breakage and rejoining of chromatid (s) and errors in kinetochore separation, respectively. The former aberration involved a dicentric bridge and an acentric fragment (BF), a chromatid loop with an acentric fragment (LF) and a double bridge with 2 fragments (BBFF); a double loop with 2 fragments (LLFF) was not seen. The chromatid bridge is usually associated with an acentric fragment, but sometimes the fragment is missing, which may be defined as a

pseudo-side-arm bridge as shown below. Configurations probably resulting from rejoining errors of broken ends, which were detected as nicked chromatids at anaphase (Fig. 2 a & b), could be sorted into this category. Misdivision of the kinetochore induces extremely anomalous configurations (e. g., DARLINGTON 1939): three examples are shown in Figure 2. They could be explained as follows: In the first case (Fig. 2 a), the kinetochore misdivision occurred at one of 4 chromatids of the C homologue, associated with a side-arm bridge between the short arms of the misdivided chromatid and one of the homologous chromatids. In the second case (Fig. 2 b) one set of paired chromatids of the E homologue separated precociously so that only one chromatid moved toward one pole and three to antipole. The third case (Fig. 2 c) is a chromatid loop configuration which occurred with the A homologue, kinetochore misdivision took place with its counterpart, and the expected fragment was missing at the same time.

None of the aberrations like extra micronuclei were detected when the first investigation was made with other (non-chilled) flower buds, viz., bud nos. I and II

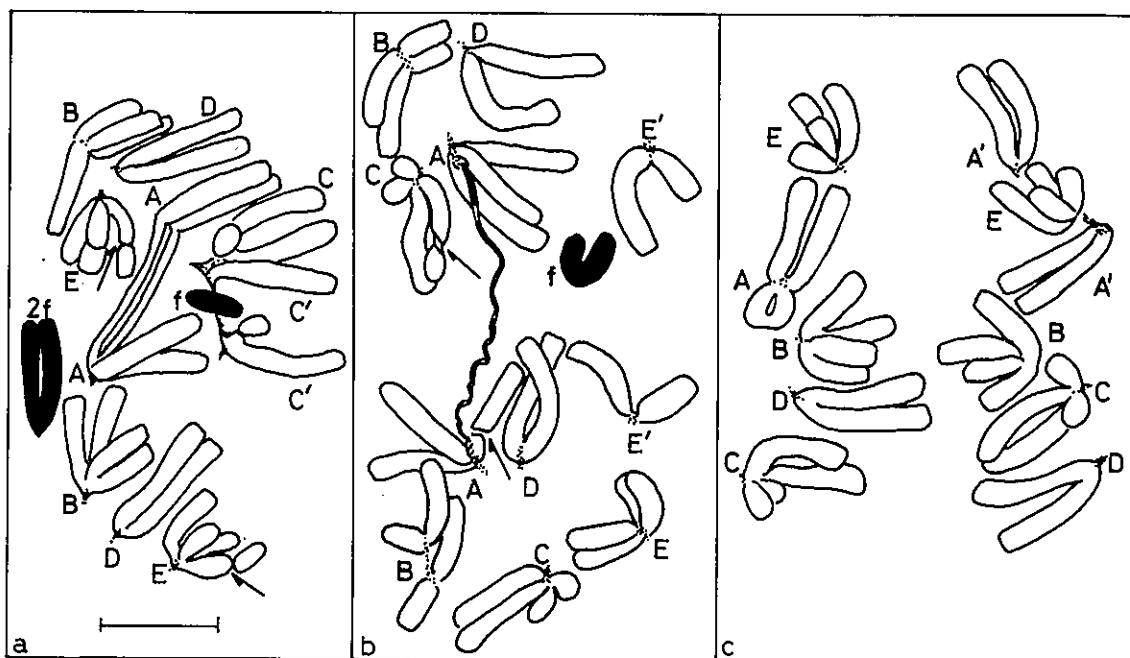


Fig. 2. Chromatid and kinetochore aberrations caused by chilling the flower bud of *T. grandiflorum*. (a) A double bridge of chromosome A associated with 2 fragments, and a single chromatid bridge of the short arm of chromosome C accompanied with misdivision, and also incomplete healing of the broken chromatid of chromosome E (arrowed). (b) A single bridge of chromosome A with a fragment, precocious separation of a paired chromatid of chromosome E and B, and incomplete healing in chromosome A and C. (c) A single loop and misdivision of its counterpart in chromosome A; acentric fragment is missing. Each primed letter denotes a single chromatid resulted from misdivision of kinetochore. Scale is 10  $\mu$ m.

Table 3. A comparison of different cytological aberrations observed in a flower bud of *T. grandiflorum*<sup>1)</sup>

Chromo some	Mean Xta	N	BF	LF	BBFF	LLFF	Break/Frag.	Desyn aptic	Mis div.	Non-disj.
A	3.32	27	8 <sup>2)</sup>	8 <sup>2)</sup>	3	0	1	0	2	1
B	2.34	50	0	0	0	0	0	0	0	0
C	1.78	39	7 <sup>2)</sup>	0	0	0	2	1	1	0
D	1.18	42	3 <sup>2)</sup>	1	1	0	0	0	3	0
E	1.15	41	1	0	0	0	5	0	3	0

1) Mean chiasmata were scored from 32 cells of anther no. 5. 50 cells of anther nos. 3 and 4 of flower bud no. III of the plant no. 4 in Table 2 were examined for the other meiotic configurations. 2) Including 1 sample of "missing fragment" in each case. Abbreviation: N (normal cells), BF (a single bridge with a fragment), LF (a single loop with a fragment), BBFF (a double bridge with 2 fragments) and LLFF (a double loop with 2 fragments).

of the same plant. This suggests that these aberrations described above may have been induced as a result of chilling the flower bud. In other words a certain meiotic stage would be sensitive to such a change in temperature, resulting in the aberrations.

#### Estimation of the duration of the meiotic stages

For assessing the sensitive stage for the aberrations, the meiotic development of each flower bud was periodically monitored under *in situ* conditions in *T. discolor* and *T. stamineum*. The examination was carried out by 17 plants of the former species and 40 plants of the latter. Figure 3 shows meiotic developments for these species. Here units of the ordinate are converted for the duration in days. The transformed figures are shown in Table 4. These estimates agree

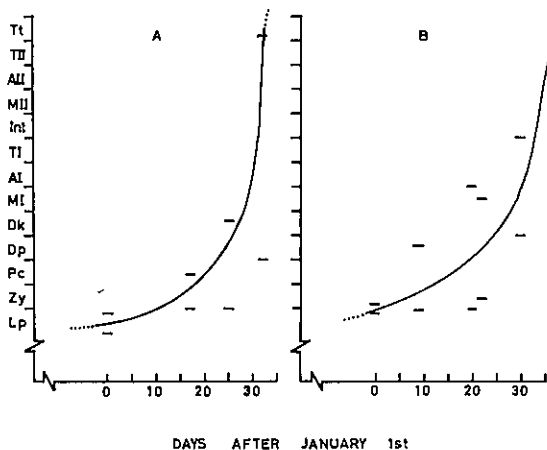


Fig. 3. Developmental stages of microsporocytes in *T. stamineum* and *T. discolor*. Ranges of the meiotic stages are shown as a pair of bars and plotted against the monitoring date. (A) *T. stamineum* and (B) *T. discolor*.

quite well with the previous reports of HOTTA and STERN (1963) and ITO and STERN (1967) in *T. erectum* L.

If these developmental time courses are applicable to microsporogenesis of *T. grandiflorum*, meiocytes ranging from mid zygonema to mid pachynema would advance to anaphase I within 2 weeks; cells exhibiting bridge and loop configurations would be at least at mid zygonema at the initiation of chilling the flower bud in a refrigerator.

#### Bridge and loop formation by a temperature shock

The transfer of flower buds from outdoor (ca. 0°C at 5 cm in depth of soil at that time) to indoor conditions (cf. Materials and Methods) may inflict a temperature shock on the meiocytes at the stages of bridge and loop formation, if they are inducible. On the basis of the stages of the longest anther examined at the initiation of the indoor cultivation, the meiotic stages of the second and the third longest anthers are predictable.

Of 20 plants with flower buds received such indoor treatment, only one exhibited bridge and loop configurations in *T. discolor*. 250 cells were examined in each anther of the plant and the data are tabulated on Table 5 and Figure 4. According to a Chi-square test, such an event is significantly uniform throughout all anthers ( $\chi^2=12.03$ ,  $df=9$  and  $p=0.30-0.20$ ). The frequency of BF is higher than that of LF; two loops with 2 fragments (LLFF) were not seen.

By another experiment of the indoor cultivation, the bridge and loop configurations were detected in meiocytes of *T. stamineum*, where a flower bud out of 15 buds contained aberrant meiocytes in all 6 anthers (Table 6 and Fig. 5). The meiotic stages ranged from anaphase I to telophase II. None of the meiocytes, ranging from metaphase II to telophase II, possessed 2

Table 4. Estimates of the duration (days) of the meiotic stages<sup>1)</sup>

Species	Lp	Zy	Pc	Dp	Dk	MI	AI	TI	Int	MII	AII	TII
<i>T. discolor</i>	55.0	7.0	5.2	3.2	1.8	1.5	0.5	0.5	—	1.5	—	—
<i>T. stamineum</i>	55.0	11.5	7.5	5.0	3.5	1.5	1.2	0.8	0.8	0.8	1.5	1.2

1) Estimated as the initiation of the stage of leptonema is on the middle of October. Abbreviation : Lp (leptotene) and see the legend of Table 2 for the others.

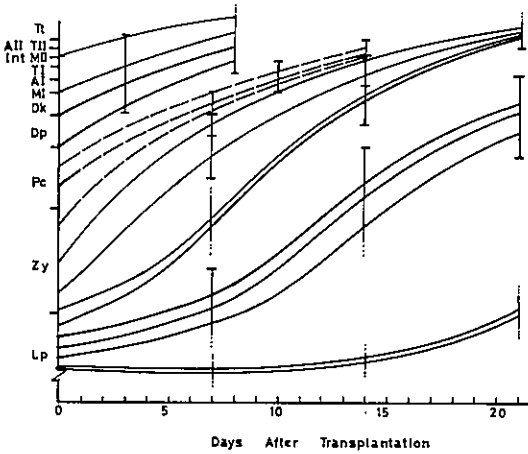


Fig. 4. Developmental stages of microsporocytes of *T. discolor* transferred into indoor cultivation at various times. Each line represents the developmental curve examined sequentially at a flower bud. Broken lines indicate the developmental curves examined at anthers which contained some meicyotes of bridge and loop configurations. The 21-, 14- and 8-day-long experiments started on Jan. 18, Feb. 1 and Feb. 8, respectively. Bars indicate the range of meiotic stages observed except for indiscernible stages shown by dotted lines.

fragments, suggesting that neither a double bridge (BBFF) nor a double loop (LLFF) took place. This agrees with the result observed at anaphase I. The ratios for normal to aberrant cells were not appreciably different among meicyotes of anther nos. 4, 5 and 6. On the other hand, the ratio of BF to LF varied drastically in anther no. 6.

It is noteworthy that some cells at the late leptotene stage were killed during the indoor cultivation. These findings agree with the results obtained by *in vitro* culture of microsporocytes (ITO and STERN 1967; ITO 1973). Following the flower buds from outdoor to indoor cultivation at late zygotene and mid pachytene stage in *T. discolor*, meicyotes possessed the bridge and loop configurations at anaphase I or II (Fig. 4). This is also true in the second flower bud of *T. stamineum* (Fig. 5 c). These observations suggest that the bridges and loops were easily induced in both cases at a certain period of the zygotene-pachytene stages, unless these configurations resulted from crossovers at inversion heterozygotes.

Another point to be interested is that the bridges and loops occurred most frequently at a particular chromosomal arm: chromosome A in *T. discolor* and the long

Table 5. Frequency distribution of meiotic stages within a flower bud and bridge and loop configurations occurred in *T. discolor*

Anther no.	Meiotic stages						Bridge and loop configuration.					Total
	Pr	Dk	MI	AI-TI	Int	M II	N	BF	LF	BBFF	LLFF	
1	—	—	—	580	420	—	—	—	(not scored)	—	—	—
2	—	—	7	872	121	—	144	75	30	1	0	250
3	—	—	101	849	50	—	160	65	25	0	0	250
4	—	101	462	437	—	—	168	57	25	0	0	250
5	48	138	483	331	—	—	150	73	24	3	0	250
6	224	276	495	5	—	—	—	—	(not scored)	—	—	—

Homogeneity: among all anthers,  $\chi^2=12.03$ ,  $p=0.30-0.20$ ; between nos. 2+3 and nos. 4+5,  $\chi^2=1.99$ ,  $p=0.70-0.50$ ; between nos. 3+4 and nos. 2+5,  $\chi^2=8.51$ ,  $p=0.05-0.02$ ; between no. 2 and no. 5,  $\chi^2=1.81$ ,  $p=0.70-0.50$ ; between no. 3 and no.4,  $\chi^2=0.71$ ,  $p=0.70-0.50$ . Abbreviation: Pr (prophase I), Dk (diakinesis), MI (metaphase I), AI (anaphase I), TI (telophase I), Int (interphase), N (normal cells), BF (bridge with a fragment), LF (loop with a fragment), BBFF (doble bridge with 2 fragments) and LLFF (double loop with 2 fragments).

arm of chromosome B in *T. stamineum* (Fig. 6), suggesting that the breakpoint may localize at a particular region of the chromosomes.

### Discussion

#### 1) Possible cause of U-type bridges and loops

Regarding the direct stimulus for the induction of the bridges and loops in *T. grandiflorum*, the most

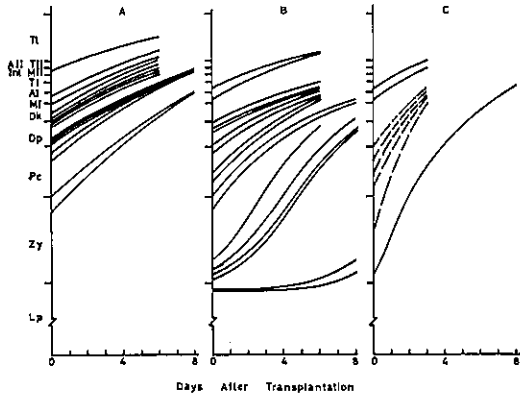


Fig. 5. Developmental stages in microsporocytes of *T. stamineum* transferred into indoor cultivation at various stages of meiosis. (A) The curves obtained from meocytes of the most advanced stage in each anther of the first (oldest) flower bud. (B) The curves from meocytes of the least advanced stage in each anther of the first flower bud. (C) The curves from meocytes of the average in advancement in each anther of the second oldest flower bud. Broken lines represent the developmental curves for meocytes in which some showed bridge and loop configurations at anaphase I.

probable one is the change of temperature ( $15^{\circ}\text{C} \rightarrow 4^{\circ}\text{C}$ ); it is also probable that the occurrence of the configurations relates to a temperature shock in *T. discolor* and *T. stamineum* ( $0^{\circ}\text{C} \rightarrow 9^{\circ}\text{C}$ ). It has been considered that physiological disturbance of meocytes leads to various damages of chromosomes and alters the modes of genetic recombination: Especially, the effects of temperature shock (MATSUURA 1937; SWANSON 1940; BARBER 1942; EMSWELLER and BRIERLY 1943; DORWICK 1957; HENDERSON 1962, 1966; MAGUIRE 1968; ERICKSON 1968; ERICKSON *et al* 1970; LU 1969; CHURCH and WIMBER 1971; BAYLISS and RILEY 1972).

There may be two alternative possibilities for temperature shock to bring about the aberrations: The first one attributes an enhancement of crossing over within the inverted segments, and another the increase in chromatid breakage and reunion irrespective of such inverted segments. The first explanation is, however, unlikely for the aberrations in *T. grandiflorum* because it requires the inverted segments in all the chromosomal pairs except the B homologue (cf. in the case of *Paris quadrifolia*, GEITLER 1937); it demands no crossing over in one flower bud and high number of crossovers in the other bud of the same plant to have taken place. The second explanation which may involve basically the same process as LEWIS' and JOHN'S hypothesis (1966), described as the 2: 1 hypothesis in the text (p. 8), is also applicable to the configurations and their frequencies. In contrast with the configurations in *T. grandiflorum*, the bridges and loops in *T. discolor* and *T. stamineum* can be explained by crossing over within the inverted

Table 6. Frequency distribution of bridge and loop configurations in *T. stamineum*

Slide no. <sup>1)</sup>	Stages observed	N	BF	LF	BBFF	LLFF	Total
1	AII - TII <sup>2)</sup>	87		13		0	100
2	AII - TII <sup>2)</sup>	67		33		0	100
3	InT - MII <sup>2)</sup>	432		168		0	600
4	AI	97	66	37	0	0	200
5	AI	122	52	26	0	0	200
6	AI	120	66	14	0	0	200

1) Corresponding to the length of anther. 2) Details were not distinguishable except bridge and micronuclei which may correspond to either one dicentric chromatid bridge with one acentric fragment or one chromatid loop with one fragment at anaphase I. Homogeneity: among all anthers,  $\chi^2=62.11$ ,  $p<0.001$ ; among anther nos. 1, 2 and 3,  $\chi^2=15.85$ ,  $p=0.01-0.001$ ; between nos. 1+2+3 and 4+5+6,  $\chi^2=42.91$ ,  $p<0.001$ .

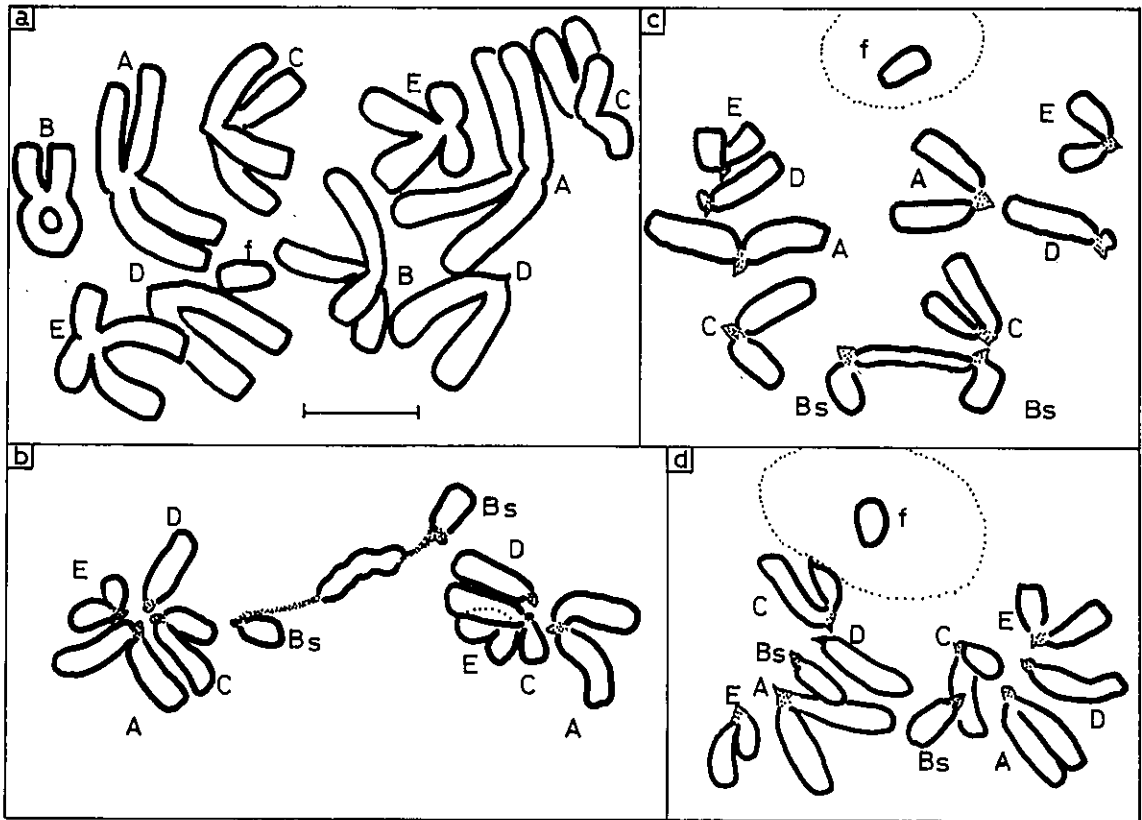


Fig. 6. Loop configurations in *T. stamineum*, showing various lengths of chromatid bridges in the long arm of chromosome B. Note rather uniform length of acentric fragment in each case. (a) Anaphase I configuration. (b) Configuration at anaphase II. (c) Normal configuration of LF-type anaphase II. (d) An LF-type anaphase II but long arms of chromosome B missing. Scale is 10  $\mu$ m.

segments, but their frequencies are more likely to be explained by adopting the 2: 1 hypothesis. At any rate that temperature shocks selectively act at mid zygonema and mid pachynema was confirmed; the thermal change of about 10°C was effective (cf. Table 8).

It was evident that anther length varies within a flower bud, which corresponds to the meiotic stages of microsporocytes (Table 5 and also cf. BENNETT *et al* 1971; WALTERS 1978). This information is rather surprising, since meiocytes within a flower bud are known to develop synchronously in *Trillium* (ITO and STERN 1967). Meiocytes may not be synchronized at all even within a flower bud; yet, the asynchrony may be indiscernible at early prophase by means of microscopy. It is therefore probable to consider that invisible minor difference in the meiotic cell stage of zygotene-pachytene was sufficient for the very fine specificity of meiotic timing affected by the difference in a temperature change, resulting in the bridge and loop configurations.

Non-random distribution of meiotic chromosomal breaks is a source of another dimension for consideration. It is a rather natural assumption that such non-random breaks are due to the localization of inverted segments within the chromosomal arms. However, NEWMAN (1966, 1967) observed in *Podophyllum* that dicentric bridges predominantly occur in chromosome E and F, in which nucleolar organizing regions are differentiated. The breakpoints may be engaged in a particular operation at the critical stage of the meiotic development, so that the chromosomal arms would be influenced easily by exposure to physiological disturbance. Configurations shown in *T. stamineum* may represent such a case.

The observation may concern geographical differentiation in plant species: Any environmental fluctuation in soil temperature may inflict meiotic development in meiocytes to bring about either sporocyte-death or conditioning in genotrophs. It is rather commonly observed that spontaneous abortion in



anthers takes place in many liliaceous as well as other plants whose meiosis initiates at early autumn. In fact, soil temperature shifts up or down even daily about 10°C at late autumn as well as in mid spring (IHARA unpublished data) when either micro- or macrosporocytes are at the time of zygotene-pachytene. Further, it was shown in *Arabis gemmifera* (Cruciferae) that a cool moist condition as a temperature shock seems to be major factor to induce the change of a hairy genotroph, if the plants with flower buds in the zygotene-pachytene stages were transferred to receive the above mentioned thermal shock and subjected to selfing (K. IHARA unpublished M. Sci. Thesis, at Univ. Tokyo).

2) *Mode of breakage and rejoining*

The model employed here is based on the following

evidence and assumption: Breakage-and-rejoining of chromatids takes place at the 4-strand stage for the BBFF to occur. It is assumed that any of the four strands can be involved in the break-and-rejoining process, and the kinds of rejoining increase as the number of broken ends increase, but they may occur equally by chance. If a U-turn rejoining occurs, it results in a dicentric chromatid with two acentric chromatids which may keep paired to show a chromosomal fragment. If a healing of the broken parts occurs directly or crossforwardly with an exchange of chromatids, it would not be detected by cytological means. However, if an imperfect healing occurs, it might be seen as a chromatid gap at anaphase I. Extreme cases are possible to consider: for example, if a 3-strand

Table 7. Results and frequencies of crossover recovered from chromatid breakage and U-turn rejoining

Type of break	Kinds of U-turn rejoining	Results
1-strand break	no U-turn rejoining	fragment only
2-strand break	1-2→L 2-3→B 1-3→B 2-4→B 1-4→B 3-4→L	BF/LF=2:1
3-strand break	1-2→L 2-3→B 1-3→B 1-3→B 2-4→B 1-4→B 2-3→B 3-4→L 3-4→L	BF/LF=2:1
4-strand break	1-2 & 3-4→L L 1-3 & 2-4→B B 1-4 & 2-3→B B	BBFF/LLFF=2:1

Table 8. Chi-square test of the observed frequencies of bridges and loops against a 2:1 hypothesis

Species	Conditions of heat shock	BF	LF	$\chi^2$	P	
<i>T. grandiflorum</i> <sup>1)</sup>	15°→4°C	A	8	8	1.99	0.20-0.10
		B	0	0	—	—
		C	7	0	3.49	0.10-0.05
		D	3	1	(0.12	0.80-0.70)
		E	1	0	—	—
<i>T. stamineum</i>	0°→9°C		66	37	0.31	0.70-0.50
			52	26	0.00	>0.90
			66	14	9.02	0.01-0.001
			184	77	1.73	0.20-0.10
<i>T. discolor</i> <sup>2)</sup>	0°→9°C		75	30	1.07	0.30-0.20
			65	25	1.24	0.30-0.20
			57	25	0.29	0.70-0.50
			73	24	3.22	0.10-0.05
			270	109	3.56	0.20-0.10

1) 3 BBFF in chromosome A and 1 BBFF in chromosome D are excluded from the test. 2) 4 BBFF are excluded from the test.

break is followed by a U-turn rejoining and an imperfect healing, a BF or LF with an *extra* fragment would be recovered. Table 7 summarizes all of the simple cases, where such conversion factors as positions and frequencies of chiasmata are not taken into consideration, because of their extremely low frequencies in North American species of *Trillium* (IHARA 1973).

The model explained above, hereafter to be referred to as the 2 : 1 hypothesis, can be tested for its reliability. Most of the observed data fit this hypothesis, though the results of 4-strand break are insufficient for the test because of low frequency (Table 8). Some data deviated significantly from the expected figures can be considered to be either due to sampling bias or due to any conversion factors. However, it is a reasonable conclusion that the breakage-and-rejoining occurred in a random process for the present materials.

The stage of zygotene-pachytene includes not only the completion of chromosomal pairing (ROTH and ITO 1967), a part of genetic crossing over (BEADLE 1932; ABEL 1965; GRELL 1966; GRELL and CHANDLEY 1965; LAWRENCE and DAVIES 1967; LAWRENCE and HOLT 1970; RHOADES 1968; LU 1969, 1974) and their associated biochemical events (e. g., HOTTA *et al* 1966; HOTTA and STERN 1971, 1974, 1976; SMYTH and STERN 1973) but also the time of U-type crossing over in *T. grandiflorum* and probably other two species, as described here.

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#### 摘 要

北米産エンレイソウ 3 種の花粉母細胞で見られた染色分体橋及び染色分体環の頻度を報告した。又、花粉母細胞の各時期のタイム・コースを記載した。そして、この様な染色分体橋や環が出現する機構について考察し、それが地理的分化の要因にもなり得ることを論じた。

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○ 馬場胤義編：佐賀県植物目録 佐賀植物友の会（佐賀市神野町三ツ溝 2384 井上英幸方），1982. 1. 23 発行。B 5 版，266 頁（内索引 25 頁）。非売品。

昭和 39 年、馬場胤義編「佐賀県生物誌植物篇」が刊行されたが、その後、17 年の間に新種 1，新変種 1，新雑種 1 が追加されたばかりでなく、分布上重要なものが発見された。しかし、一方では近年の開発により、失った種類も多く、現状を記録した改訂版の必要性から本書が生れることになった。今回も亦編集を馬場さんが引受けられたが、同氏は 80 をこえる御高齢とうけたまわるにつけ、本書にかける御熱意にはただただ敬服の他はない。この結果、昭和 56 年 10 月現在で、佐賀県に確認できた羊歯植物以上の高等植物の総数は 2068 種（品種を除く）で、旧目録にくらべると 200 種ばかり増加している。これは全く驚くべきことで、佐賀植物友の会の会員の方々の熱意の結晶であるに違いない。その何よりの証拠は、この会が昭和 40 年 4 月に発足し、以来毎月例会が続けられ、昭和 56 年 11 月に第 200 回記念例会が開催されたということで明白である。

○ 大場達之（解説）・平野隆久（写真）：フィールド百科 山と溪谷社（〒105 東京都港区芝大門 1-1-33）発行。このシリーズは、野の花 1, 2, 3; 山の花 1, 2, 3 の 6 冊からなるもので、既に山の花 3 を残して 5 冊が刊行されている。最終的に日本の野草 825 種がカラー写真で紹介される予定である。各冊 19.8 × 20.5 cm. 156 頁。1,700 円。

○ 植松春雄著：山梨の植物誌 井上書店（東京都文京区京郷 6-2-8），1981. 3. 30 発行。18 × 26 cm, 595 頁（内索引 43 頁）。15,000 円。

同じ著者によって昭和 33 年に出版された同名の書の改訂増補版である。本書の中心となる高等植物目録は、271 頁より 525 頁までの 255 頁に及び、著者はここ 10 年程、主として東京国立科学博物館に通いつづけたという。（里見信生）