**Chromosome Studies in Cyperaceae, III. The maturation divisions
in *Scirpus lacustris* L., with special reference to the
heteromorphic pairing¹⁾**

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(With 47 text-figures and 25 photomicrographs)

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The chromosome number of *Scirpus lacustris* L. was reported by Håkansson (1928) and Kostrionkoff (1930) to be $n = 21$ and by the writer (1937a) to be $n = 19$ in the PMC's. In the writer's materials was observed one large compound chromosome which was not found in the case of other investigators. In the writer's previous paper (1937a) it was predicted that the compound chromosome may be composed of three chromosomes, though there was no cytological evidence. Recently he (1938) reported three types of *Scirpus lacustris*: one type is the normal self-colored form, *S. lacustris* L. var. *typicus* Honda (this plant was used as *S. lacustris* L. in the previous paper, 1937a) with the chromosome constitution of $n = 19 = 18s + 1S_6$, $2n = 38 = 36s + 2S_3$, and other two types are variegated, *S. lacustris* L. var. *typicus* Honda f. *pictus* Honda and *S. lacustris* L. var. *Tabernaemontani* Trautv. f. *zebrinus* Makino²⁾, with the chromosome constitution of $2n = 40 = 39s + 1S_3$, $2n = 42s$ respectively, where S designates the compound chromosome and s the small ones. Between these types we can find gradual changes as regards to the compound chromosomes in fine correlation with the phenotypic characters and these changes in the chromosome constitution were considered from the view point of segmentation (1938). So the chromosome behaviour in the maturation divisions of these variegated forms would have much significance to see whether the previous prediction is fulfilled by the cytological evidence. If the compound chromosome conjugates with any small elements during the maturation division some heteromorphic pairing should be met with. Heteromorphic chromosome pairs have been the subject of many studies, on account of their significance for an understanding

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2) Throughout the present paper these three types will be referred to as *typicus*, *pictus* and *zebrinus*, respectively.

of meiosis and of the relationship of chromosome behaviour to the genetic phenomena.

In the present paper, meiotic details of the two types *pictus* and *zebrinus*, mainly of the former, will be described.

Materials and Methods

Materials used in the present investigation were taken from the two variegated forms, *pictus* and *zebrinus*.

The inflorescences were fixed with Carnoy's fluid for a few hours. They are preserved in 75% alcohol, after being washed in 95% alcohol. From the preserved inflorescences the anther sacs were taken out with needles under the magnifying-glass and stained with aceto-carmin. The cover-glass was sealed with vaseline.

Observations

Meiosis of *Pictus*

I-Metaphase. As already mentioned *pictus* has 39 small chromosomes and one large compound one in the root-tip cells. If the large compound chromosome is homologous or has, at least, some homologous parts with 3 small chromosomes, there would arise a heteromorphic chromosome pair in the maturation divisions. In facts, many different heteromorphic pairs composed of large compound chromosomes and 1 to 3 small ones have been observed as expected. In the I-metaphase 18 to 25 chromosomal elements, varying in size, were clearly counted, the frequency of which is shown in table 1.

Table 1

Nos. of elements	18	19	20	21	22	23	24	25	Total
Frequency	1	8	88	262	42	9	2	2	414
%	0.24	1.93	21.26	63.29	10.15	2.17	0.48	0.48	

As the somatic chromosome number of this form is 40, one should generally find 20 bivalents in the first meiotic metaphase in case there are no abnormalities in the chromosomal constitution. The wide variation in the number of chromosomal elements in the first divisions of this species is chiefly caused by the occurrence of unpaired univalent and heteromorphic multivalent. The most frequent cases are those consisted of 18 bivalents, 2 univalents and one heteromorphic polyvalent.

Various types of heteromorphic polyvalents, consisting of one compound chromosome and 1 to 3 small univalents, as well as various number of univalents, varies 1 to 10, have been observed. In the paper of 1938 it has been stated that the compound chromosome may be equivalent to 3 small chromosomes; if this is true they should conjugate with one another owing to their homology, if not entirely homologous along the whole length, and would result in various heteromorphic multivalents.

A). In 5 of 414 PMC's studied 19 chromosomes were observed of which 18 were bivalents and one was a conspicuously larger chromosome. In text-figs. 1 and 2 (cf. photo 1), we can distinguish 18 bivalents and one large element. The latter is understood as a compound multivalent composed of one compound chromosome (S) and 3 small ones (3s). These two cases may be referred to as $n = 19 = 18_{II} + (1S + 3s)^*$. If some gemini have failed to pair, there arises univalents in the first meiotic metaphase; fig. 3 shows one of such cases, consisting of 17_{II} , $1(1S + 3s)$, and 2 univalents. Other possible chromosomal configurations which contain $(1S + 3s)$ were also observed, i.e. $(1S + 3s) + 16_{II} + 4_I$ and $(1S + 3s) + 15_{II} + 6_I$.

B). S conjugates with 2s (figs. 4-8). Two types of conjugation between S and 2s were observed, i.e. s-S-s type (figs. 4, 6, 7; photo 3) and S-2s (figs. 5, 8; photos 2, 5). The former type, always characterised by two constrictions, is prevalent than the latter. Out of 414 PMC's, 107 cells were found to contain the complex multivalent $(1S + 2s)$; the following four cases were observed:

$(1S + 2s) + 18_{II} + 1_I$	...	86 cells	(figs. 4, 5; photos 2, 3)
„ $+ 17_{II} + 3_I$	...	14	„ (fig. 6)
„ $+ 16_{II} + 5_I$	...	5	„ (fig. 7)
„ $+ 15_{II} + 7_I$	...	2	„ (fig. 8; photo 5).

These conditions support very strongly the previous assumption (1938) concerning the possibility of 3s chromosomes to come from 1S.

C). The commonest type was one consisted of 18 bivalents, $(1S + 1s)$, and 2 univalents (figs. 9-12). In these cases S and s were usually clearly identified by way of constriction. Following five cases were distinguished:

$(1S + 1s) + 18_{II} + 2_I$	...	244 cells	(fig. 9; photo 6)
„ $+ 17_{II} + 4_I$	...	29	„ (fig. 10; photo 7)
„ $+ 16_{II} + 6_I$	...	5	„ (fig. 11)
„ $+ 15_{II} + 8_I$	...	2	„ —
„ $+ 14_{II} + 10_I$	...	2	„ (fig. 12).

* Hereafter the compound chromosome and small ones will be referred to as S and s, respectively, and $(1S + ns)$ indicates a compound multivalent consisting of 1S and ns (where $n = 0, 1, 2, 3$, rarely 4, 5).

D). The compound S chromosome sometimes failed to pair with any small chromosomes. Several cases were observed:

(1S)+19_{II}+1_I ... 2 cells (fig. 13)
 „ +18_{II}+3_I ... 4 „ (fig. 14)
 „ +17_{II}+5_I ... 2 „ (fig. 15).

All cases described above are the possible and expectable formulae which can be derived from the conception that the compound chromosome S is equivalent to 3 small ones. Rather exceptional cases, however, were also observed.

Figs. 1-20. Various configurations of the I-metaphase of *pictus* (cf. table 2). 1-3. I-group; 1 and 2, (1S+3s)+18_{II}. 3, (1S+3s)+17_{II}+2_I. 4-8. II-group; 4 and 5, (1S+2s)+18_{II}+1_I. 6, (1S+2s)+17_{II}+3_I. 7, (1S+2s)+16_{II}+5_I. 8, (1S+2s)+15_{II}+7_I. 9-12. III-group; 9, (1S+1s)+18_{II}+2_I. 10, (1S+1s)+17_{II}+4_I. 11, (1S+1s)+16_{II}+6_I. 12, (1S+1s)+14_{II}+10_I. 13-14. IV-group; 13, (S)+19_{II}+1_I. 14, (S)+18_{II}+3_I. 15, (S)+17_{II}+5_I. 16-20. V-group; 16, 1_{IV}+18_{II}+2_I. 17, (1S+1s)+1_V+16_{II}+1_I. 18, [(1S+1s)+1_{II}]+17_{II}+1_I. 19, 2(1S+1s)+15_{II}+1_{IV}. 20, 20_{II}+2_I. $\times 1700$.

E). Exceptional cases. Some of them are illustrated in figs. 16-20. Fig. 16 shows a case of 18_{II}+2_I+1_{IV}. A ring bivalent is seen among them. In fig. 17 (cf. photo 8), 16_{II}, 1_I, 1_V and 1 (1S+1s) are present. Fig. 18 (cf. photo 9) presents 17_{II}, 1_I and 1 multivalent which is probably composed of s-S and 1 bivalent by loose conjugation. In fig. 19 (cf. photo 10) we can see 3 large elements, judging from their figures, 2 of them lying parallel may be (1S+1s) and the rest a tetravalent. Fig. 20 shows no large element, but only 20_{II} and 2_I.

All chromosome associations observed in the first meiotic metaphases are summarized in table 2.

Table 2. Chromosome associations observed in the first meiotic metaphases

	Chromosome associations	Number of elements	Frequency of PMC's	%
I	(1S+3s)+18 _{II} (figs. 1, 2)	19	5	1.93
	„ +17 _{II} +2 _I (fig. 3)	20	1	
	„ +16 _{II} +4 _I	21	1	
	„ +15 _{II} +6 _I	22	1	
II	(1S+2s)+18 _{II} +1 _I (figs. 4, 5)	20	86	25.85
	„ +17 _{II} +3 _I (fig. 6)	21	14	
	„ +16 _{II} +5 _I („ 7)	22	5	
	„ +15 _{II} +7 _I („ 8)	23	2	
III	(1S+1s)+18 _{II} +2 _I („ 9)	21	244	68.12
	„ +17 _{II} +4 _I („ 10)	22	29	
	„ +16 _{II} +6 _I („ 11)	23	5	
	„ +15 _{II} +8 _I	24	2	
	„ +14 _{II} +10 _I („ 12)	25	2	
IV	(1S) +19 _{II} +1 _I („ 13)	21	2	1.93
	„ +18 _{II} +3 _I („ 14)	22	4	
	„ +17 _{II} +5 _I („ 15)	23	2	
V	20 _{II} +2 _I („ 20)	22	2	2.17
	19 _{II} +1 _{IV}	20	1	
	18 _{II} +2 _I +1 _{IV} („ 16)	21	1	
	17 _{II} +4 _I +1 _{IV}	22	1	
	17 _{II} +1 _I +1 _{VII} („ 18)	19	2	
	(1S+1s)+16 _{II} +1 _I +1 _V („ 17)	19	1	
	2(1S+1s)+15 _{II} +1 _{IV} („ 19)	18	1	
	Total		414	100

I-Anaphase. The segregation of heteromorphic chromosomes has been the subject of many studies, since the differences between the pairs are favourable to detect their behaviour. In the present case, however, owing to the minuteness and ill-staining condition of the chromosomes, a precise observation of this stage has not been made. But the following few facts were found:

(1) The compound (1S + ns) pairs segregate slowly (figs. 21, 22, photo 11).

(2) Sometimes the compound pairs undergo non-disjunction (figs. 23, 24, photo 12).

(3) Univalent chromosomes may either go to the poles at random or divide themselves after segregation of the bivalents.

Many different heteromorphic compound multivalents observed in the I-metaphase may result in various different types of segregation, but owing to the difficulties described above, precise observations could not be made as to whether the original bulk of the compound chromosomes (S) and the attached small chromosomes separate reductionally, or they segregate equationally. Judging from the I-ana-, II-meta- and II-anaphasic configurations, however, the

heteromorphic compound multivalents in the present case may segregate rather equationally as for the chromatid segments which were distally located in respect to crossing-over. This point will be referred to more precisely later on (p. 549). A total of 114 cells at this I-anaphase stage were observed; in 110 cells the heteromorphic pairs have segregated normally, that is, probably one half of the chromatin mass to one pole and the other to another poles; in 4 cells non-disjunction has been observed. In all cases, it was hardly able to distinguish the elements, so that the difference between the separating two halves could scarcely be recognized. Observations in the second division, however, would supply something about this point. Two types of non-disjunction (figs. 23 and 24, photo 12) have been observed; in three cases out of 114 cells two attached halves failing to separate went together to one pole, in only one case two halves which had already been separated went to the same pole separately (fig. 23).

II-Metaphase. Formation of the II-metaphase plates were usually disturbed and the chromosome count was very difficult. This was chiefly due to the irregular behaviour of the probably divided univalents in the first division. Only 16 cases were analysed, of which in 5 cases the chromosome elements were counted in two sister metaphase plates. Fig. 25 is the one of these rare cases, showing both metaphase plates, one containing 20 chromosomes with no large element and the other containing 20 chromosomes with one large element. In fig. 26 two sister plates are shown, one containing 19 chromosomes with one large element and is accompanied by 2 small chromosomes which are lying outside the equatorial plate, the other containing 18 with one large element and is accompanied by 4 small chromosomes lying outside the plate. These small chromosomes are perhaps the divided univalents in the first division. Observations of the II-metaphases are tabulated in table 3. In table 3 A, (+) in the right column denotes a sister nucleus in which the presence of the large chromosome has been recognized. The number italicized shows the number of chromosomes which are lying outside the equatorial plate. Those cases with — after the parentheses denote that the observation has been made in only one sister plate. Rather high frequency of those cases without S may be attributed to the small number of observations. In fact, the observations in the II-late metaphase showed in only 8 cases out of 93 observed PMC's the large element presented in one of the sister plates, and in the rest 85 cases it was present in both plates. Only from the chromosome associations of the II-metaphase it was quite difficult to presume in what manner the segregation of the chromosome set was made, because, the first, to recognize the constitution of the large elements in

the second metaphase was impossible and, in the second, a number of segregation types could be arisen from the complicated chromosomal constitution in the I-metaphase. Out of only 20 cases in which the chromosomal elements could be counted (table 3 B), 14 cases contained the large element. Most frequent cases were (19s + 1S).

II-Anaphase. In the II-anaphase a comparatively high degree of irregularities such as occurrence of chromatin bridges or the lagging

chromosomes were observed. Out of 70 observed cells, 46 cells were including the laggards, 5 cells the chromatin bridge, and 19 cells normal. At this stage the distribution of the large element was mainly noticed. Owing to the difficulties only 30 cells were analysed. In 6 cells 2 large elements were observed in only one of a pair sets, while in 24 cases the large element was in both sister sets. Such chromosomal constitution as observed in the former cases, may probably be derived from either non-disjunction of the large element or the reductional separation of the compound multivalent in the first or second group (in table 2). The reductional separation will be done if no chiasma is formed between the compound chromosome and the small element or elements. In the latter 24 cases, chromatin bridges were observed in 3 daughter nuclei, all of these were composed of the large element. Occurrence of laggards was rather frequent, appearing in 30 daughter nuclei, of which in 9 cases the laggards have contained the large element. A small number of chromosomes being outside the plate were also observed in 4 daughter nuclei.

II-Telophase. The occurrence of chromosomal bridges and laggards in the II-anaphase and in the II-telophase are shown in table 4. As is seen in the table, percentage of chromatin bridges and laggards in the later stage changed to 8.2%, 36.9%, respectively. Consequently the total percentage of irregularities decreases as the stage proceeds. This fact is due mainly to the arrival of the laggards to either pole in the II-telophase, since the chromatin bridges are persistent.

Table 3. Chromosome association in the second metaphase

A	(18s+1S)+(18s+1S)	(19s+1S)–		
	(20s)+(19s+1S)	(18s+1S)–		
	(18s+1S)+(20s)	(19s+1S)–		
	(18s+1S+2)+(17s+1S+4)	(20s+1)–		
	(19s+1S)+(+)–	(19s+1S+1)–		
	(20s+1)+(+)–	(18s+3)–		
	(21s)–	(18s+1S+2)–		
	(19s+1S)–	(19s+1S)–		
Number of chromo- somes		Frequency		Total
		with S	without S	
B	18	1	1	2
	19	4	0	4
	20	9	4	13
	21	0	1	1
Total		14	6	20

Table 4

	II-Anaphase	II-Telophase
Chromatin bridges	5 cells (7.1%)	6 cells (8.2%)
Laggards	46 „ (65.7%)	27 „ (36.9%)
Normal	19 „ (37.2%)	40 „ (54.9%)
Total	70	73

Separation of the chromosomes in the II-telophase has shown much irregularities, i.e. the laggards and chromatin bridges were observed in relatively high frequency in the well observed 19 cells.

Figs. 21-34. The I-ana-, II-meta-, II-ana- and the II-telophase of *pictus*. 21 and 22, early I-anaphase. 23 and 24, late I-anaphase showing two types of non-disjunction of the large chromosome. 25 and 26, II-metaphase. 25, two sister metaphase plates, one having 20 chromosomes with one large element, the other having 20 chromosomes but with no large one. 26, two sister metaphase plates, one having 21 chromosomes with one large and 2 precession chromosomes, the other having 22 chromosomes with one large and 4 precession chromosomes which are drawn in blank. 27-30, II-anaphase. 27, two sister sets, showing segregation of heteromorphic pairs, in one of which a probable non-disjunction of the pair is shown. 28, the frequent case, in both sets segregation of the heteromorphic pairs can be seen. 29, comparatively frequent case, showing also segregation of the heteromorphic pairs. 30, large chromosomes go to the pole at random. 31-34, chromatin bridges in the II-telophase. 31, the most frequent bridge type. 32, chromatin bridge broken in one end. 33, chromatin bridge in one set, and laggards in the other. 34, chromatin bridge in each set. Both bridges are consisted of large chromosomes. $\times 1500$. (figs. 30 and 31 $\times 1700$).

That the chromatin bridges are always consisted of the large chromosomes is noteworthy.

As a result of these irregularities during the maturation division, there may arise various daughter nuclei containing quite different chromosomal elements. Unfortunately the pollen grain division has not been observed, so the direct evidence for the resulting daughter nuclei having various chromosome numbers has not been obtained. However, the velocity of development of one survival nucleus was much low, while in general the differentiation between them takes place rapidly. Probably, owing to the unbalanced chromosomal condition, even the survival nucleus out of the four would fail to develop. In this year (1938), all inflorescences have shooted their stigma but failed entirely to shed their pollen.

Meiosis of *zebrinus*

As already mentioned, *zebrinus* has 42 small chromosomes in the root-tip cells. In the I-metaphase, chromosome counts varied 19 to 22; these were summarized in table 5.

Table 5. Chromosome counts in the I-metaphase in *zebrinus*

Nos. of chromosomes	19	20	20+1f	21	21+1f	22	Total
Frequency	3	19	5	168	1	4	200

I-Metaphase. Most frequent counts are of 21, as expected. Equatorial plane formation was rather normal, and 168 PMC's (84%) out of observed 200 PMC's have contained 21 chromosomes, in which one is somewhat larger than the rest (fig. 37). Unexpected number, 19 and 20, were also observed in 3 and in 19 cells respectively. Fig. 35 shows 19 chromosomes with 2 rather larger elements. Fig. 36 shows 20 chromosomes containing 2 rather larger elements. In fig. 38, 21 bivalents and a small fragment, and in fig. 39, 20 bivalents and 2 univalents are observed.

I-Anaphase. Separation of the chromosomes in the I-anaphase is carried on rather regulary and out of 109 cells observed only 2 cells have contained 1-2 laggards, while the remaining 107 cells have included neither laggards nor chromatin bridges. The laggards observed in the I-anaphase might have been derived either from unpaired univalents or from fragments.

II-Metaphase. Chromosome counts in the II-metaphase were not easy, because of rather irregular formation of the metaphase plate. Sometimes, separation of the elements was also disturbed by the irregular orientation of the elements. One of such disturbed

Photos. 1-25. 1-10. The I-metaphase of *pictus*. 1, $(1S+3s)+18_{II}$ (cf. text-fig. 1). 2-3, two types with configuration $(1S+2s)+18_{II}+1_I$ (cf. text-figs. 4, 5). The former contains a compound multivalent with S-2s constitution, the latter a compound multivalent with s-S-s constitution. 4, $(1S+2s)+17_{II}+3_I$. 5, $(1S+2s)+15_{II}+7_I$ (cf. text-fig. 8). 6, $(1S+1s)+18_{II}+2_I$. (cf. text-fig. 9). 7, $(1S+1s)+17_{II}+4_I$. (cf. text-fig. 10). 8, $(1S+1s)+16_{II}+1_I+1_v$. (cf. text-fig. 17). 9, $1_{VII}+17_{II}+1_I$. (cf. text-fig. 8.1) 10, $2(1S+1s)+1_{IV}+15_{II}$. (cf. text-fig. 19). 11-12. The I-ana- and telophase of

side view is shown in fig. 40, in which 3 elements stand entirely excluded from the equatorial plane. Fig. 41 shows one laggard.

II-Telophase. 102 PMC's, i.e. 204 II-telophase were observed. In 193 daughter nuclei normal separations with neither laggards nor chromatin bridges have been observed. The remaining 11 daughter nuclei have contained a few laggards.

Figs. 35-45. I-metaphase of *zebrinus*. 35, 19 chromosomes with 2 rather large ones. 36, 20 chromosomes with one rather large one. 37, the most frequent configuration with 21 bivalents, one of which is larger than the rest. 38, 21 bivalents and a small fragment. 39, 22 chromosomes, probably including 2 univalents. 40, early II-anaphase, 3 chromosomes are lying outside the plate. 41, II-telophase, one lagging chromosome presents. 42-45, metaphases of the primary nuclear division of the pollen grain. 42, 18 chromosomes with 2 larger ones. 43, 19 chromosomes with no large ones. 44, 20 chromosomes present; one larger chromosome presents in a, while in b no such large ones. 45, 21 chromosomes; a, A-type having one large element; b, B-type. $\times 1700$. (figs. 40 and 41 $\times 1500$).

Pollen grain division. As a result of the irregularities observed in the maturation division, various pollen grains with different

pictus. 11, the large chromosome segregates slowly (cf. text-fig. 21). 12, non-disjunction of the large chromosome. 13-15. Meiosis of *zebrinus*. 13, I-metaphase, the most frequent case with 21 bivalents (cf. text-fig. 37). 14, II-anaphase, 3 chromosomes are lying outside the plate (cf. text-fig. 40). 15, telophase of the primary pollen nuclear division; chromatin bridge is seen (cf. text-fig. 46). 16-25. The I-ana-, II-ana- and II-telophase of *pictus*. 16, irregular separation of chromosomes at I-anaphase; in the left cell, non-disjunction of the large chromosome is seen. 17, II-anaphase; note the heteromorphic chromosome (cf. text-fig. 29). 18, II-telophase; chromatin bridge in one set, and laggards in the other (cf. text-fig. 33). 19a, b. Sister plates of a PMC at different foci. Note the segregation of the heteromorphic chromosomes (cf. text-fig. 28). 20, II-anaphase, showing segregation of the heteromorphic chromosome. 21, II-anaphase (cf. text-fig. 27). 22, II-anaphase (cf. text-fig. 30). 23-25, chromatin bridges (cf. text-figs. 31, 34, 32). $\times 1200$ (photo 16, $\times 700$; photo 22, $\times 1300$).

chromosomal elements may be found. In fact the chromosome counts in the primary nuclear division of pollen grains ranged from 18 to 22 (table 6). Of 68 pollen grains observed, 55 (80.8%)

Table 6. Chromosomal configuration in the pollen grain division

Number of chromosomes	18	19	20	21	22	Total
Frequency of A-type	1	0	1	21 (30.8%)	0	23
„ „ B-type	0	1	8	34 (50.0%)	2	45
Total	1	1	9 (13.2%)	55 (80.8%)	2	68

have consisted of 21 chromosomes; of which 21 pollen grains have contained one large element (A-type) (fig. 45a), while 34 pollen grains have contained no such large element (B-type) (fig. 45b). Thus pollen grains are divided into two types, A- and B-types, according to the presence of the large element. Fig. 44a shows a plate of A-type containing 20 chromosomes with 2 large ones, and fig. 44b a plate of B-type also containing 20 chromosomes but without any large one. Rather abnormal plates consisting of either 18 with a few rather elements or 19 with no larger elements are shown in figs. 42 and 43, respectively..

Chromosomal irregularities are also observed in the anaphase of the primary nuclear division of pollen grains. Out of 22 observed pollen grains, 3 pollen grains had definite chromatin bridges and 2 pollen grains contained some lagging chromosomes (fig. 46.)

Figs. 46, 47. 46, telophase of the primary pollen nuclear division of *zebrinus*. Two chromatin bridges are seen. Three degerating nuclei are lying in a narrow end of the cell. 47, various pollen grains. a, b and c are viable, the rest being abortive.

As a result of irregularities in meiosis, many abortive pollen grains (62.4%) with various shapes have been made (fig. 47). There are also some variations in size among the pollen grains with healthy appearance.

The percentage of such pollen grains (37.6%) is accord with that (37.5%) of the pollen grains containing 21 chromosomes of the A-type to the whole pollen grains containing 21 chromosomes (A-type + B-type). This seems to show that the pollen grains of the A-type are normal.

Discussion

Investigation of the maturation divisions of *pictus* and *zebrinus*, though it is yet imperfect, would offer some evidence for the previous prediction that the large chromosome first found in *typicus* and then in *pictus* may be a compound chromosome which is equivalent to 3 small chromosomes (Tanaka, 1938). In the first meiotic division of *pictus*, a number of various chromosomal associations were met with (cf. table 2). The most frequent were consisted of 18 bivalents, 2 univalents and a compound multivalent which was considered as composed of one compound chromosome and a univalent attached to it.

The existence of the first group in table 2, which can be expressed in $(1S + 3s) + (15 + n)_{II} + (6 - 2n)_I$ where $n = 0 - 3$, would support the prediction previously presented. The second group can be expressed in a formula $(1S + 2s) + (15 + n)_{II} + (7 - 2n)_I$ where n varies 0 to 3. The most frequent association of this group was given when $n = 3$; in this case each of the 2 small elements (univalents) usually attach to each end of the compound chromosome. These 2 attached univalents would be scarcely homologous to each other. Rarely, however, these 2 elements attach to each other and conjugate with the compound chromosome at its one end. Third group can be expressed in a formula $(1S + 1s) + (14 + n)_{II} + (10 - 2n)_I$ where n varies 0 to 4. In this group one small element attaches to the proximal end of the compound chromosome. The most frequent case is given when $n = 4$, that is $(1S + 1s) + 18_{II} + 2_I$, and is interesting in the point of non-conjugation of the remaining 2 free univalents. Consequently, when one out of 3 components conjugates with the compound chromosome the rest fail to conjugate to each other. The fourth group with a formula of $(1S) + (17 + n)_{II} + (5 - 2n)_I$, where n varies 0 to 2, is a rather rare case of small percentage (ca. 1.93% in total). When n takes the value of 1, the most prevalent case is given, i.e. $(1S) + 18_{II} + 3_I$. This case would supply an evidence that the 3 components would scarcely be homologous to each other.

The other remaining cases are of less frequent and probably of abnormal ones.

Fragmentation and fusion. Considering the four groups above mentioned it may be reduced that the large chromosome is equivalent to 3 small chromosomes. Similar mode of conjugation is reported in *Lycoris albiflora* Koidz. by Inariyama (1932) and in *Nothoscordum fragrans* Kunth (= *Allium fragrans* Vent.) by Levan (1935) and Levan and Emsweller (1938). In *Lycoris* there are 17 chromosomes, consisting of 5 V-shaped and 12 rod-shaped, in diploid num-

ber. In meiosis the V-shaped chromosome conjugates loosely with 2 rod-shaped chromosomes at each distal end resulting a heterotrivalent. In *Allium*, a normal diploid form has 16 median chromosomes in somatic cells, while in a diploid form with $2n = 18$ studied by Levan (1935) 4 terminal chromosomes instead of 2 long biarmed ones, and in a form of $2n = 19$ studied by Levan and Emsweller (1938) 6 terminal chromosomes instead of 3 long biarmed ones. These terminal chromosomes have about the same length as one arm of the long biarmed chromosomes and in meiosis occasionally 2 terminal chromosomes conjugate with one median chromosome at each distal end forming a heterotrivalent. In these cases, the phenomenon has been explained that the 2 smaller elements must be at least partly homologous with the larger chromosome, since one is paired distally with one arm of the larger, and the second is similarly paired with the other arm. The relationship between the elements has been explained as following; in *Allium* the terminal chromosomes have originated by fragmentation of the biarmed ones, while in *Lycoris* in a reverse way i.e. by fusion. In the present case of *Scirpus*, the second group meets with the first category, and the same explanation could be adopted. However, the present case is different in its complicated association, viz. the large chromosome conjugates with 3 small chromosomes as shown in the first group and this is conclusive to the prediction that the large chromosome is equivalent to 3 small chromosomes. It will be noteworthy to refer to the conception of fragmentation and fusion which have been considered to be important factors in chromosome evolution in order to get correct idea. Instances reported in connection with the conception of fragmentation and fusion are the following:

Fragmentation; *Oenothera* (Lutz, 1916; Hance, 1918), *Zea* (Kuwada, 1919), *Lolium* $\times$ *Festuca* (Peto, 1933), *Campanula* (Marchal, 1920), *Secale* (Gotoh, 1924), *Carex* (Heilborn, 1924), *Crepis* (Navashin, 1925, 1931; Babcock and Lesley, 1926), *Lycoris* (Inariyama, 1932), *Nothoscordum* (Levan, 1935; Levan and Emsweller, 1938), *Scilla* (Satô, 1935), *Drosophila* (Metz, 1914), *Lymantria* (Seiler and Haniel, 1921), *Solenobia* (Seiler, 1922), *Gryllodea* (Ohmachi, 1935).

Fusion; *Chorthippus* and *Chloealtis* (Robertson, 1916), *Hesperotettix* and *Mermiria* (McClung, 1905, 1914, 1917), *Drosophila* (Morgan, 1922), *Lepidoptera* (Beliajeff, 1930), *Crocus* (Mather, 1932), *Cardamine* (Lawrence, 1931), *Nicotiana* (Vilmorin and Simonet, 1928), *Crepis* (Navashin, 1926), *Jamaicana* (Woolsey, 1915), *Fritillaria* (Darlington, 1930), *Vicia* (Sharp, 1914; Sakamura, 1915; Sweshinikova, 1928), *Scilla* (Satô, 1936), *Lycoris* (Take-

naka, 1931), *Stenobothrus* (Darlington and Dark, 1932), *Phragmatobia* (Seiler and Haniel, 1921), *Felis* (de Winiwarter, 1934), *Gryllotalpa* (de Winiwarter, 1927; Barrigozzi, 1933).

The fragmentation-fusion hypotheses, however, as Navashin (1932) has emphasized, encounters the fundamental difficulty. That is, it is a well known fact that a chromosome can function both in meiosis and in somatic mitosis only when it possesses the kinetic body or kinetochore (Delauney, 1930; Metzner, 1894; S. Navashin, 1916; Trankovsky, 1930; M. Navashin, 1931). Since each chromosome has only one kinetochore, fragmentation can never produce more chromosomes than there are kinetochores, viz. fragmentation is unable of increasing the chromosome number unless new kinetochores are added or developed de novo. Recently the constancy of kinetochore has been proved experimentally (Dobzhansky, 1931; M. Navashin, 1931a; Mather and Stone, 1933). Dobzhansky (1931) in *Drosophila*, M. Navashin (1931) in *Crepis*, studying the variations experimentally produced by X-rays, have showed that fragments of any size may be detached from any chromosome but they do not survive unless they retain the kinetochore or rejoin another chromosome or fragment possessing it. As to the de novo formation of kinetochore, a few instances are known, that is in *Crepis* (Navashin, 1926) and in *Tradescantia* (Darlington, 1929). These cases, however, according to Navashin (1932), are less conclusive. Hence, if indeed they occur at all, they must be exceedingly rare.

Fusion of entire chromosomes should produce new chromosomes possessing more than 2 kinetochores. Rare occurrence of such new chromosomes, however, may be due to instability of their structure. In the X-rayed materials studied by Dobzhansky (1931) and Navashin (1931), fusion of entire chromosomes has not been observed. In the X-rayed *Crocus*, Mather and Stone (1933) have observed fragmentation and end-to-end fusion, and very occasionally lateral fusion in the somatic cells. In this case fusion has generally occurred between the distal segments and other whole chromosomes or proximal fragments (translocation), and as to the fusion of 2 whole chromosomes or 2 proximal fragments or one of them, which gives rise a double attachment chromosome, actual cases were consisted of 2 fused proximal fragments. However, "it may be hypothetically assumed that chromosomes with kinetic constrictions very close to one end may fuse without any deleterious effect; such assumption, though not improbable, awaits, however, as yet its proof" (Navashin, 1932). Rare instances of the fusion of whole chromosomes, the so-called compound chromosomes, are peculiar only to certain animals, and the "attached X-chromosomes" in *Drosophila*.

Consequently Navashin's dislocation hypothesis seems most supportable, and in this case fragmentation and fusion can not be considered as simple as applied in usual cases. But since such a process of dislocation must be need of several generations to occur and there may be a tendency of disappearance of chromosomal abnormalities caused by fragmentation and fusion in gametogenesis, it may be of little significance that such a process may give rise new chromosomal constitutions in gametogenesis. But if such a process takes place in somatic cells, fragmentation and fusion in Navashin's sense could occur, and more likely produce progeny possessing new chromosomal constitutions. In *Crocus* (Mather, 1932) and in *Scirpus* (in this paper), however, it is very probable that these have gone on.

Thus the present case, in the light of the known cases, it will be one of the rare cases where fusion of three chromosomes has first occurred in rhizome, and then redisorganization has occurred; the very small size of chromosomes would have favoured to this process. Unexpected chromosome numbers observed in the I-metaphase and in the metaphase of the pollen grains of *zebrinus* may support this assumption, and *zebrinus* might have arisen by redisorganization of the compound chromosomes in *typicus* or *pictus*.

Chromatin bridges. Occurrence of chromatin bridges in plants has very often been reported by many authors, and is recently summarized by Emsweller and Jones (1938). In the known cases, usually chromatin bridges have occurred in the first division and rather rarely in the second division as well as in the pollen grain division. Instances in which the chromatin bridges in the second division have been observed are the following:

Untreated species; *Zea* (Beadle, 1929), *Aucuba* (Meurman, 1929), *Allium* (Sinotô, 1936), *Trillium* (Smith, 1935), *Tradescantia* (Sax, 1937), *Fritillaria* (Frankel, 1937), *Narcissus* (Fernandes, 1937).

Species hybrids; *Godetia* (Chittenden, 1928), *Aegilops* (Micznski, 1931), *Crepis* (Müntzing, 1934), *Pisum* (Håkansson, 1936), *Lilium* (Richardson, 1936; Ribbands, 1937), *Tricyrtis* (Sinotô and Satô, unpublished).

Irradiated stocks; *Nicotiana* (Goodspeed and Avery, 1933), *Vicia* and *Tradescantia* (Mather, 1934).

Chromatin bridges observed in somatic mitosis:

Untreated species; *Lilium* and *Narcissus* (microspore) (Emsweller and Brierly; Emsweller; unpublished, but cited in Emsweller and Jones, 1938).

Irradiated stocks; *Crocus* and *Tulipa* (Mather and Stone, 1933).

Exposed to low temperature; *Rhoeo* (Derman, unpublished, cited by Emsweller and Jones, 1938).

The occurrence of chromatin bridges in meiosis and somatic mitosis are of great significance, since these bridges must have derived from the double attachment chromosomes. Such chromosomes with double attachments have been observed in many plants cited above, under the natural condition, in species or generic hybrids, and also in irradiated materials. Explanations as for the occurrence of chromatin bridges have been made fundamentally on the conception of inversion and crossing-over. In *Trillium erectum*, Smith (1935) has explained the chromatin bridges observed in both the first and the second division by crossing-over within the inversion region. By a single crossing-over within the inversion region, a fragment devoid of kinetochore and a chromatid with two "non-sister" kinetochores which forms a bridge at anaphase are given. When there are 2 chiasmata one within the inversion region and one proximal to it, a "loop" type arises which results in bridge formation in the second division. Richardson (1936), studying the structural hybridity in *Lilium Martagon album* $\times$ *L. Hansonii*, has illustrated many possible cases which would form the chromatin bridges in both first and second division. In these favourable materials, the authors have gained the clear explanation. Chromatin bridges in the second division have been considered to occur either from the "loop" types or from the persistent dicentric chromatid which by chance reached to the same pole. Emsweller and Jones (1938) have offered "unusual crossing-over" to explain the chromatin bridges in both the first and the second division and also in the microspore division. Sax (1937), in *Tradescantia*, has observed dicentric chromosomes in the microspore division, and he suggested that the dicentric chromosomes are formed by the reunion of sister chromatids which had broken in the meiotic mitosis.

In the present case of *Scirpus*, both crossing-over and unusual crossing-over must have occurred. The most frequent bridge types observed in the second division, one of which is seen in fig. 33, must be derived from the second group (in table 2) in which usually 2 small chromosomes attach distally to the large chromosome at both ends. When 2 chiasmata, one in the proximal and the other at the distal end, are formed a double attachment chromatid arises, which results in the bridge formation in the second division (diagram C). A very rare and curious bridge type is shown in fig. 34, where both bridges are consisted of the compound chromosomes, and may be understood if we explain such pairing to be that 2 small chromosomes attach to the distal ends of the compound one and further one more

element undergoing unusual crossing-over attaches to the another chromatid at the middle portion (diagram D). In *zebrinus* no chromatid bridges have been observed both in the first and the second division except in the pollen grain division. In the last case, it is probable that the large chromosome or chromosomes which have been observed in the pollen grain metaphases might have occurred by fusion of 2 or more chromosomes in the former meiosis, consequently double attachment chromosomes might have occurred and survived until the pollen grain division. In every cases, one or two fragments must arise, but no such distinguishable fragments were observed. This is probably due to the minuteness of them as well as the chromosome themselves.

Segregation of heteromorphic chromosome. Heteromorphic chromosome pairs have been studied to account for the segregation mode in meiosis and the relationship of chromosome behaviour to genetic phenomena. Robertson (1915) has observed pre-reduction in unequal bivalents in *Tettigidea* and *Acridium*. Wenrich (1916), however, has reported in *Phrynotettix* that the pre- and post-reduction have occurred in the same frequency in a heteromorphic bivalent. Carothers (1926, 1931) has reported a varying ratio of pre- to post-reduction in *Trimerotropis*, *Mecostethus*, and in *Amphitornis*. Since the time, Stern (1931) and Creighton and McClintock (1931), in *Drosophila* and *Zea mays*, respectively, have proved the parallel correlation between cytological crossing-over and genetics, this problem has become also dealt with by that conception. Belling (1931b), in

Diagrams A-D. Explanation in text.

Aloe, has shown that the separation of a heteromorphic bivalent was conformed with expectation on the conception of crossing-over, and at the same time has reported that the observations of the earlier authors can be explained in good accordance with this hypothesis.

Huskins and Spier (1934), in *Triticum*, have reported both reductional and equational separations, with predominant frequency in the former. The first equational divisions of heteromorphic bivalents have been explained as due to crossing-over. Mather (1933) has fully discussed the theoretical results of the chiasma frequency on the mode of chromatid disjunction. Matsuura (1938) has reported, in *Trillium*, clear evidence for both reductional and equational separations in meiosis, which based upon his 'Neo-two-plane' theory. Haga (1937) has reported similar mode of separations in *Paris*.

In the present case of *Scirpus*, 3 types of heteromorphic chromosome pair were observed. The most frequent type, (1S + 1s), in the third group (in table 2), usually performs 'equational' separation concerning the unpaired segment, in the presence of a single chiasma at the proximal part (diagram B). These equationally separated chromatids in the first division show the type of reductional separation in the second division as shown in fig. 28. If no chiasma is formed between the elements, the first division will be reductional (diagram A). From the configurations observed in the II-metaphases, i.e. cases lacking the large element, this type of separation must have also occurred.

Segregation of chromosomes in two frequently observed types of (1S + 1s) + 18_{II} + 2_I and (1S + 2s) + 18_{II} + 1_I will be briefly referred to. In table 7, all possible configurations are included, excluding the cases which are possible theoretically, but not observed actually. Calculated frequency (table 8) obtained from table 7 is accord with that obtained in table 3. This fact may indicate that univalents observed in the first division behave quite irregularly, viz. sometimes divide themselves in the first division and sometimes pass to the pole, as it is true, at random.

Table 8. Calculated frequency of various types obtained from table 7

Number of chromosomes	Calculated frequency		Total
	with S	without S	
19	7	2	9
20	18	3	21
21	10	4	14
Total	35	9	44

Fertility. Test of goodness of pollen grains of 3 types is the following; *typicus*, 99.81% good, *pictus*, 0%, *zebrinus*, 37.6% good. From the present data it is difficult to interpret the relationship between these types, especially that of the second to both the first and the last. The second type shows an exceedingly high degree of structural hybridity. This fact is suggestive to know the origin of *pictus* which however demands further investigations.

Table 7. Segregation of chromosomes of $(1S+1s)+18II+2I$ and $(1S+2s)+18II+1I$ in the first division. Number in parenthesis shows that of the elements; + and - indicate the presence or absence of large chromosome. S' or S'' denotes large elements. Cases denoted with * are to be calculated twice in estimation of frequency.

Chromosome configuration		(1S+1s)+18II+2I				(1S+2s)+18II+1I				
Mode of separation	one chiasma		no chiasma		2 chiasmata		one chiasma		no chiasma

Univalent divides itself in the first division	$S'+18+2(\frac{1}{2})$ (21+)	$S'+18+2(\frac{1}{2})$ (21+)	$S+18+2(\frac{1}{2})$ (21+)	$18+1+2(\frac{1}{2})$ (21-)	$S''+18+(\frac{1}{2})$ (20+)	$S'+18+(\frac{1}{2})$ (20+)*	$S+18+(\frac{1}{2})$ (20+)	$2+18+(\frac{1}{2})$ (21-)		
	$S'+18+1$ (20+)*	$S'+18+1$ (20+)*	$S+18+0$ (19+)	$18+1+2$ (21-)	$S''+18+0$ (19+)	$S'+18+0+1$ (20+)*	$S+18+0$ (19+)	$2+18+1$ (21-)		
	$S'+18+0$ (19+)	$S'+18+2$ (21+)	$S+18+1$ (20+)	$18+1+1$ (20-)	$S''+18+1$ (20+)	$S'+18+1+1$ (21+)*	$S+18+1$ (20+)	$2+18+0$ (20-)		
Univalent does not divide in the first division and distribute freely, as it is			$S+18+2$ (21+)	$18+1+0$ (19-)			$S+18+1+0$ (20+)	$1+18+1$ (20-)		
							$S+18+1+1$ (21+)	$1+18+0$ (19-)		

Summary

1). The maturation divisions of *Scirpus lacustris* L. var. *typicus* Honda f. *pictus* Honda ($2n = 39s + 1S$) and of *S. lacustris* L. var. *Tabernaemontani* Trautv. f. *zebrinus* Makino ($2n = 42s$) have been described. The first plant *pictus* having one large compound chromosome in a somatic cell, has shown a sort of heteromorphic pairing in the first meiotic division as expected. The last form *zebrinus* has shown rather regular meiosis.

2). In the I-metaphase of *pictus* a number of chromosomal configurations have been observed (cf. tables 1, 2); namely, in the first group (i) the compound chromosome S has conjugated with 3 small chromosomes (3s), giving a formula $(1S + 3s) + (15 + n)_{II} + (6 - 2n)_I$ where $n = 0 - 3$; in the second group (ii) S has conjugated with 2 small chromosomes (2s), giving a formula $(1S + 2s) + (15 + n)_{II} + (7 - 2n)_I$ where $n = 0 - 3$; (iii) in the third group, S has conjugated with only one small chromosome (s), $(1S + 1s) + (14 + n)_{II} + (10 - 2n)_I$ where $n = 0 - 4$; (iv) in the fourth group, S has failed to conjugate with any small chromosomes, $(1S + 0) + (17 + n)_{II} + (5 - 2n)_I$ where $n = 0 - 2$; (v) in the fifth, several abnormal cases were also observed. In case of *zebrinus*, the first division being rather regular, the chromosome counts in the I-metaphase were made easily; 168 PMC's (84%) out of 200 observed were consisted of 21 bivalents.

3). The compound multivalents formed in the first division of *pictus* have shown various mode of segregation in the I-anaphase. This heteromorphic pairs have segregated equationally as well as reductionally, according to the number of chiasmata between the compound chromosome and the univalents attached to it. Lagging chromosomes were observed now and then. The compound multivalents have always separated slowly. This is probably caused by the chiasma formation.

4). Chromosome counts in the II-metaphase were difficult. However, a few of them obtained have given some hints to the behaviour of the univalents and of the heteromorphic pairing. Judging from the tables 3 and 7, the univalents observed in *pictus* may sometimes divide themselves in the I-metaphase, and sometimes pass to the poles at random as it is in fact.

5). In the II-anaphase of *pictus*, remarkable structural hybridity, i.e. formation of chromatin bridges, occurrence of the lagging or precession chromosomes were observed. Chromatin bridges have been considered to have produced from the results of both crossing-over and unusual crossing-over between the compound chromosome

and 1-3 small chromosomes attached to the former. Generally, chromatin bridges have been formed in the first division and rarely in the second. But in the present case, the conditions were entirely reversed, i.e. they were not observed in the first division but only in the second.

6). In the II-telophase of *pictus*, chromatin bridges were persistent. However laggards should have reached to the poles in time to be included, for the percentage of the cells containing laggards had decreased as the stage proceeds.

7). As a result of irregularities during the meiosis, there must arise various pollen grains containing varied chromosomal constitutions. Unfortunately, the pollen grain division was observed only in *zebrinus*, where the chromosome numbers counted have varied 18 to 22.

8). Test of goodness of pollen grains of 3 types, i.e. *typicus* (normal self-colored), *pictus* (variegated form), and *zebrinus* (variegated form), has shown 99.81% good for *typicus*, 0% for *pictus*, and 37.6% good for *zebrinus*.

9). From the present karyological observations it has been shown that the large chromosome in *pictus* is equivalent to 3 small chromosomes which were usually non-homologous to each other. As for the origin of the large chromosome, the conception of "fragmentation and fusion" in Navashin's sense has been applied.

10). It is worthy to note that only *pictus*, one of the variegated forms, shows a high degree of structural hybridity, in spite of the close relationship among these 3 forms. This question, however, waits a further analysis.

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