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Differential transmission of extra genome chromosomes in pentaploid blueberry

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Summary. Transmission of extra genome chromosomes by three *Vaccinium ashei* ($2n=6x=72$)/*V. corymbosum* ($2n=4x=48$) pentaploid hybrids backcrossed to the hexaploid species *V. ashei* was examined. Chromosome numbers were determined for 36 and 31 progeny representing $5x \times 6x$ and $6x \times 5x$ type crosses, respectively. Chromosome numbers ranged from hypopentaploid ($2n=4x+11=59$) to hexaploid with means of $2n=66.2$ for $5x \times 6x$ progeny and $2n=68.0$ for $6x \times 5x$ progeny, representing overall extra genome chromosome gains of 3.3% and 33.3%, respectively. Extra chromosome number distributions for both the $5x \times 6x$ and $6x \times 5x$ progeny deviated significantly from the theoretical distribution assuming random chromosome transmission and were also found to be heterogeneous. The $2n=5x+9=69$ class predominated in $6x \times 5x$ progeny, while a predominate class was lacking in the $5x \times 6x$ progeny. Higher than expected frequencies of plants with chromosome numbers near the pentaploid and hexaploid levels were found in the $5x \times 6x$ progeny, whereas the frequency was only greater at the hexaploid number in $6x \times 5x$ progeny. Present and previous results (Vorsa et al. 1986) indicate that extra genome chromosome transmission in oddploids can be influenced by selection at both gametophytic (pollen) and post-zygotic stages. However, post-zygotic selection may involve two different mechanisms acting concurrently: 1) chromosome imbalance due to aneuploidy and/or 2) endosperm imbalance referring to maternal: paternal genome ratios deviating from 2:1. Such a mechanism could result in differential transmission rates of extra genome chromosomes in oddploids when crosses are made to differing ploidy levels, and to reciprocal differences as well.

Key words: Blueberry – Pentaploid hybrid – Extra chromosome transmission – Aneuploidy – Endosperm imbalance

Introduction

The extent to which extra genome chromosomes are transmitted in oddploids, triploids and pentaploids in particular, has been found to be species dependent, and in certain cases, dependent on whether the oddploid is utilized as the pollen or seed parent. Extra chromosome transmission is severely limited through both the pollen and seed in species such as tomato (Lesley 1928), *Datura* (Satina et al. 1938), and *Lotus pendunculatus* (Chen and Grant 1968). Consequently, mostly diploids and primary and secondary trisomics are recovered. Reciprocal differences in extra chromosome transmission have also been observed (Punyasingh 1947). Triploids of *Pyrus* (Darlington and Moffet 1930) and *Populus* (Johnsson 1940) exhibit greater transmission through both pollen and seed, although an overall loss of extra genome chromosomes still exists compared to random chromosome transmission. Bimodal chromosome number distributions have been observed for some species (Levan 1936, 1942; Punyasingh 1947; Janick et al. 1959) when triploids are used as pollen parents and in $3x \times 2x$ crosses of potato (Vogt and Rowe 1968). Genotype is a factor influencing extra chromosome transmission in pentaploid wheat (Kaltsikes et al. 1970; Zhirov and Ternovskaya 1979).

Since developing trisomic series has been the focus of many studies, triploids have generally been crossed only with diploids. Thus, few studies (Alston and Jones 1968; Thompson and Cameron 1928) have examined transmission of the extra genome chromosomes in oddploid crosses to both lower and higher even number ploidy levels. In *Dianthus caryophyllus* (Brooks and Mehlquist 1961) and alfalfa (Binek and Bingham 1970; Blake and Bingham 1986) transmission of the extra genome chromosomes in triploids was reduced in crosses to diploids, but was found to be enhanced in crosses to tetraploids.

Table 1. Progeny type, progeny identification number, parentage, and number of plants sampled for eight backcross progenies, *V. ashei/V. corybosum* pentaploid hybrids backcrossed to *V. ashei*, used in cytological study

Identification no.	Parentage[a]	No. plants sampled
5x×6x progenies		
7237	(Weymouth×Woodard) no. 7×Tifblue	10
7235	(Woodard×Weymouth) no. 1×Woodard	10
7384	(Woodard×Weymouth) no. 1×Tifblue	6
7245	(Darrow×Tifblue) no. 1×Woodard	10
Total		36
6x×5x progenies		
7246	Tifblue×(Woodard×Weymouth) no. 1	11
7250	Woodard×(Woodard×Weymouth) no. 1	5
7247	Tifblue×(Darrow×Tifblue) no. 1	10
7251	Woodard×(Darrow×Tifblue) no. 1	5
Total		31

[a] Pentaploid hybrids are given in parentheses. Tifblue and Woodard represent *V. ashei* ($2n = 6x = 72$) cultivars and Darrow and Weymouth represent *V. corymbosum* ($2n = 4x = 48$) cultivars

Cultivated forms of blueberry exist at two ploidy levels: a tetraploid species ($2n = 4x = 48$), *Vaccinium corymbosum* L., and a hexaploid species ($2n = 6x = 72$), *Vaccinium ashei* Reade. As a result, bilateral gene exchange between these two ploidy levels in blueberry has been of great interest. Hybrids between these two species are pentaploids (Jelenkovic and Draper 1973), which when backcrossed to the tetraploid species give progenies having a high frequency of aneuploids (Vorsa et al. 1986). Extra genome chromosome losses of 31.7% and 13.3% were noted for 4x×5x and 5x×4x progeny types, respectively. The purpose of this study was to examine transmission of the extra genome chromosomes of pentaploid *Vaccinium* in backcrosses to the hexaploid species and compare it with the transmission observed in backcrosses to the tetraploid species reported on previously (Vorsa et al. 1986). These studies could provide insight into the selective mechanisms which influence extra chromosome transmission in oddploids.

Materials and methods

Eight backcross progenies derived from three *V. ashei/V. corymbosum* pentaploid hybrids backcrossed to the hexaploid species *V. ashei* were examined cytologically (Table 1). Four 5x×6x and four 6x×5x progeny types are represented.

Budwood was collected in January of 1985, 1986 and 1987. The basal portions of cut canes were placed in flasks of water and forced at approximately 20°C. Method of bud fixation, pollen mother cell (PMC) extraction, and cytological preparation are given in Vorsa et al. (1986). Chromosome counts were made on a minimum of 15 PMC's per plant: counts were made on 3–5 PMC's from a minimum of three buds sampled at random. Counts were generally made during anaphase I,

Table 2. Chromosome number of progeny from four 5x×6x and four 6x×5x progenies representing *V. ashei/V. corymbosum* pentaploid hybrids backcrossed to *V. ashei*

Cross type	Progeny	No. plants sampled	Chromosome no (2n)													
			60	61	62	63	64	65	66	67	68	69	70	71	72	Mean
5x×6x																
	7235	10	2[a]	1	0	1	1	0	1	1	1	2	0	0	0	64.6
	7237	10	0	0	1	0	1	0	1	2	0	3	1	1	0	67.4
	7245	10	0	0	0	1	1	2	3	2	1	0	0	0	0	65.7
	7384	6	0	0	0	0	0	1	1	0	2	1	1	0	0	67.7
Subtotal		36	2	1	1	2	3	3	6	5	4	6	2	1	0	66.2
6x×5x																
	7246	11	0	0	0	0	0	1	1	1	1	3	3	1	0	68.5
	7247	10	0	0	1	0	0	1	1	1	0	3	1	2	0	67.9
	7250	5	0	0	0	0	0	0	0	1	1	3	0	0	0	68.4
	7251	5	0	0	0	0	2	0	1	0	1	0	0	0	1	66.8
Subtotal		31	0	0	1	0	2	2	3	3	3	9	4	3	1	68.0
Total		67	2	1	2	2	5	5	9	8	7	15	6	4	1	67.0

[a] Note: one plant hypopentaploid ($2n = 4x + 11 = 59$)

since at this stage interpretation of paired chromosomes during metaphase I or previous stages is avoided.

Results

Chromosome number distributions, progeny means, means of 5x×6x and 6x×5x crosses, and the overall mean are given in Table 2. Consistant chromosome counts were observed for each plant suggesting that mixoploidy was not a factor in this study. Chromosome numbers ranged from hypopentaploid, $2n=4x+11=59$, to hypohexaploid, $2n=5x+11=71$, for 5x×6x progeny and from hyperpentaploid, $2n=5x+2=62$, to hexaploid for 6x×5x progeny (Table 2, Fig. 1). The $2n=5x+9=69$ class predominated (Fig. 1c) in 6x×5x progeny, whereas a conspicuously predominate class in 5x×6x progeny was lacking.

Each cross was tested as to fit to the distribution expected assuming random transmission of the extra genome chromosome – the binomial $(0.5+0.5)^{12}$. Distributions of all four 5x×6x progenies did not differ significantly at the $P=0.05$ level, whereas distributions of three of four 6x×5x progenies (7246, 7247, and 7250) were significantly different (analyses not given). Progeny means varied from $2n=64.6$ (7235) to $2n=68.5$ (7246).

Overall means for 5x×6x and 6x×5x progeny were $2n=66.2$ and 68.0, respectively, representing 3.3% (5x×6x) and 33.3% (6x×5x) gains of extra genome chromosomes as compared to $2n=66$ expected from random transmission. The mean for the entire backcross population (Total mean in Table 2) was $2n=67.0$. Overall extra chromosome number distributions for both 5x×6x and 6x×5x progeny differed significantly from the distribution expected if transmission were at random, and were also determined to be heterogeneous (Table 3). The 5x×6x distribution displayed a higher

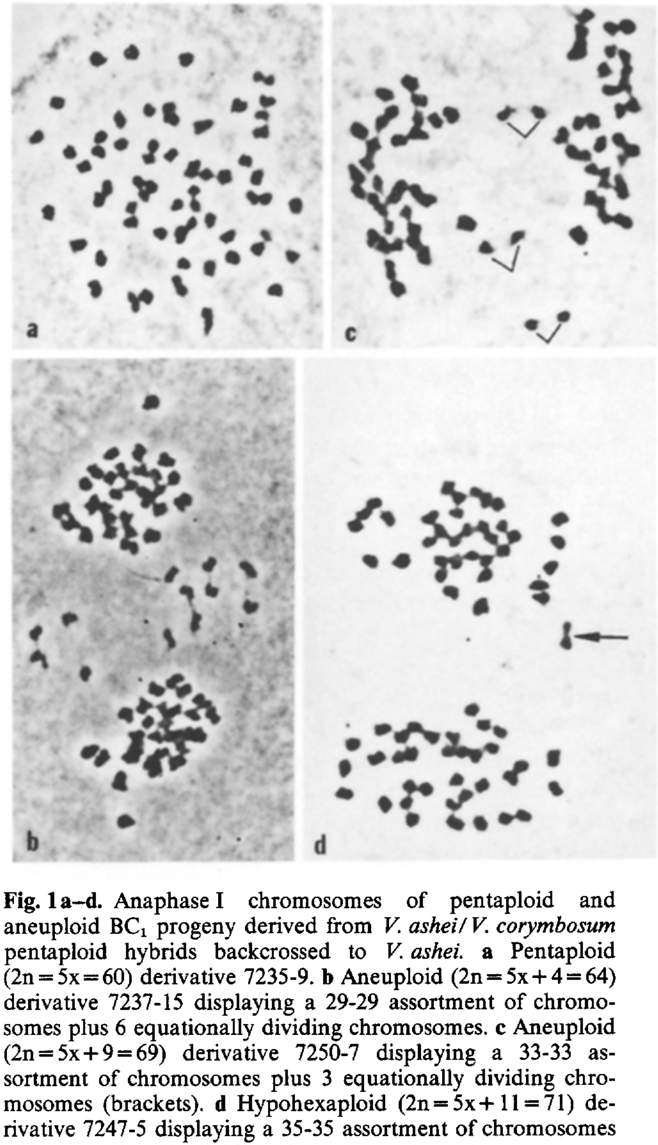

Fig. 1a–d. Anaphase I chromosomes of pentaploid and aneuploid BC_1 progeny derived from *V. ashei*/*V. corymbosum* pentaploid hybrids backcrossed to *V. ashei*. **a** Pentaploid ($2n=5x=60$) derivative 7235-9. **b** Aneuploid ($2n=5x+4=64$) derivative 7237-15 displaying a 29-29 assortment of chromosomes plus 6 equationally dividing chromosomes. **c** Aneuploid ($2n=5x+9=69$) derivative 7250-7 displaying a 33-33 assortment of chromosomes plus 3 equationally dividing chromosomes (brackets). **d** Hypohexaploid ($2n=5x+11=71$) derivative 7247-5 displaying a 35-35 assortment of chromosomes plus 1 equationally dividing chromosome (*arrow*)

Table 3. Extra chromosome number distributions in 5x×6x and 6x×5x progeny and their fit to expected binomial distribution $(0.5+0.5)^{12}$ assuming random extra chromosome transmission

Progeny	Extra chromosome no.								D.F.	$\chi^{2\,a}$	P
	0–3	4	5	6	7	8	9–12				
5x×6x											
Obs.	6	3	3	6	5	4	9				
Exp.	2.63	4.32	6.95	8.14	6.95	4.32	2.63		6	18.74	<0.005
6x×5x											
Obs.	1	2	2	3	3	3	17				
Exp.	2.26	3.72	5.98	7.01	5.98	3.72	2.26		6	95.20	<0.001
								Total:	12	113.94	<0.001
								Pooled:	6	96.13	<0.001
								Homogeneity:	6	17.81	<0.01

[a] χ^2 calculated with Yate's correction factor

than expected frequency of plants nearing both pentaploid and hexaploid levels, whereas the frequency was greater only at the hexaploid level for the 6x×5x distribution (Table 3).

Two pentaploid hybrids (Darrow×Tifblue no. 1 and Woodard×Weymouth no. 1) were crossed reciprocally with both *V. corymbosum* and *V. ashei.* Mean transmission of extra chromosomes in a progeny varied from 4.1 (progeny 73107) to 7.9 (progeny 7247) for pentaploid Darrow×Tifblue no. 1 giving a 92.6% difference, and from 4.5 (progeny 73113) to 8.5 (progeny 7246) for pentaploid Woodard×Weymouth no. 1 (88.9% difference). Parentage of progenies 73107 and 73113 are given in Vorsa et al. (1986). Although crosses were not designed to test genotypic influence of the backcross parent on extra chromosome transmission, the same pentaploid crossed in the same direction to two different genotypes (progeny 7384 vs. 7235) indicates that genotype of the backcross parent may also be a factor in extra chromosome transmission.

Discussion

To determine if lack-of-fit was due to simply a shift in the distribution, fit to the binomial distribution was retested with values for p and q representing mean gain and loss of extra genome chromosomes, respectively (Table 4). The observed 5x×6x distribution deviated significantly from the excepted. Frequency of plants with chromosome numbers nearing the pentaploid, extra chromosome class (0–1), and hexaploid, extra chromosome classes (9–12), levels was higher than expected with the discrepancy being greatest at the hexaploid level (Fig. 2). Fewer than expected plants had intermediate extra chromosome numbers, classes (4–8). The observed 6x×5x distribution did not differ significantly at the $P=0.05$ level from the expected distribution where p and q equalled 0.67 and 0.33, respectively. Nevertheless, a tendency remained for a higher than expected frequency of plants having chromosome numbers near the pentaploid and hexaploid levels. In 4x×5x and 5x×4x crosses (Table 5, Fig. 2) deviation was similar excepting that greater discrepancies occured at the tetraploid level.

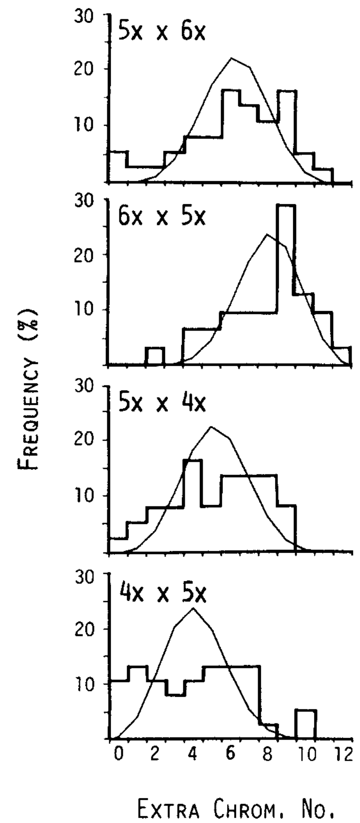

Fig. 2. Observed (*thick line*) versus theoretical (*thin line*) distributions of extra chromosomes in 5x×6x, 6x×5x, 5x×4x, and 4x×5x BC_1 progeny derived from *V. ashei*/*V. corymbosum* pentaploid hybrids. Theoretical distributions utilized p and q values corresponding to mean extra chromosome gain and loss for the respective progeny types

Table 4. Extra chromosome number distributions in 5x×6x and 6x×5x progeny and their fit to the binomial distribution of $(p+q)^{12}$, where p and q equal the mean frequency of extra chromosome gain and loss, respectively, in the respective progenies

Progeny	Extra chromosome no.											D.F.	$\chi^{2\,a}$	P
	0–1	2	3	4	5	6	7	8	9	10	11–12			
5x×6x														
Obs.	3	1	2	3	3	6	5	4	6	2	1			
Exp.[b]	0.17	0.78	2.41	3.71	6.39	8.05	6.39	5.02	1.53	0.42	0.08	6	15.6	< 0.05
6x×5x														
Obs.	0	1	0	2	2	3	3	3	9	4	4			
Exp.[c]	0.00	0.01	0.10	0.44	1.43	3.38	5.84	7.39	6.64	4.03	1.73	6	8.5	0.25–0.10

[a] χ^2 calculated with Yate's correction factor; brackets represent classes combined for χ^2 analysis

[b] Where $P=0.52$ and $q=0.48$

[c] Where $P=0.67$ and $q=0.33$

Table 5. Extra chromosome number distributions in 5x×4x and 4x×5x progeny and their fit to the binomial distribution of $(p+q)^{12}$, where p and q equal the mean frequency of extra chromosome gain and loss, respectively, in the respective progenies

Progeny	Extra chromosome no.											D.F.	χ^{2a}	P
	0–1	2	3	4	5	6	7	8	9	10	11–12			
5x×4x														
Obs.	3	3	3	6	3	5	5	5	3	0	0			
Exp.[b]	0.26	1.49	3.82	6.62	8.16	7.34	4.85	2.33	0.79	0.19	0.03	7	15.4	< 0.05
4x×5x														
Obs.	9	4	3	4	5	5	5	1	0	2	0			
Exp.[c]	1.81	4.46	7.73	9.04	7.52	4.56	2.03	0.66	0.15	0.02	0.00	6	37.3	< 0.001

[a] χ^2 calculated with Yate's correction factor; brackets represent classes combined for χ^2 analysis

[b] Where $P=0.34$ and $q=0.66$

[c] Where $P=0.44$ and $q=0.56$

These findings suggest that gain or loss of extra genome chromosomes in these four progeny types only partially accounts for the deviation from the distribution representing random extra chromosome transmission. The platykurtic nature of the 5x × 6x, 5x × 4x, 4x × 5x distributions likely contributed to the significant deviation (Fig. 1).

Deviation from random transmission of extra genome chromosomes can result from: 1) meiotic chromosome elimination (Satina and Blakeslee 1937a, b; Makino 1974), and 2) selection against aneuploid gametophytes (Thompson and Armstrong 1932), seed (Satina et al. 1938), and sporophytes (Khush 1973a). Chromosome elimination of extra genome chromosomes does not appear to be a factor in blueberry (Vorsa et al. 1986), which should result in the extra chromosome number distribution of the gametes to approach that of the theoretical. However, selection against pollen having intermediate extra chromosome numbers gives a distribution inverted to that of the theoretical (Thompson and Armstrong 1932) due to sensitivity of pollen to unbalanced chromosome numbers (Khush 1973a). This mechanism is a factor in extra chromosome transmission in blueberry as evidenced by the reduced pollen stainability found in blueberry pentaploids (Jelenkovic and Draper 1973) and hypopentaploids (Vorsa et al. 1987). However, recovery of aneuploids with intermediate extra chromosome numbers is indicative of incomplete selection. Since selection may not be as great against aneuploid female gametophytes (Khush 1973a; Singh et al. 1984), crosses where the pentaploid is utilized as the female may better refelct extra chromosome number distribution in gametes. This is perhaps why both the 5x × 6x (Table 3) and 5x × 4x (Vorsa et al. 1986) distributions more closely resemble the theoretical random curve where p and q are 0.5 (Fig. 2). This finding also lends additional support to the cytological observations that meiotic chromosome elimination in pentaploid blueberry is not of great significance. Reduced vigor and morphological abnormalities common to aneuploids of other species (Khush 1973b) were not associated with aneuploids of this study, suggesting that aneuploidy per se of the zygote or sporophyte is not a selective factor between tetraploid and hexaploid levels in blueberry.

Post-zygotic selection against aneuploidy has been established (Satina et al. 1938), however, post-zygotic selection can also operate in heteroploid crosses. Johnston et al. (1980) hypothesized that seed abortion in heteroploid crosses arises from maternal : paternal genome ratios of endosperms deviating from the optimal ratio of 2 : 1. Since the gametic chromosome number of pentaploid blueberry ranges from n = 2× to n = 3×, it is conceivable that both chromosome imbalance of aneuploid gametes and endosperm imbalance resulting from union of heteroploid gametes act concurrently in influencing extra chromosome transmission. In pentaploid crosses the maternal : paternal genome ratio will depend on: 1) the number of extra genome chromosomes in the gamete from the pentaploid, 2) ploidy of the other parent, and 3) the direction of the cross. As the chromosome number (n) of the gametes of the pentaploid increases from 24 to 36, the endosperm ratio increases from 1.33 : 1 to a more favorable ratio of 2 : 1 in 5x × 6x crosses and decreases from 3 : 1 to 2 : 1 in 6x × 5x crosses. With crosses to the tetraploid the reverse is true. As the chromosome number of the gametes of the pentaploid increases, the ratio will increase from 2 : 1 to the less favorable ratio of 3 : 1 in 5x × 4x crosses, and will decrease from 2 : 1 to 1.33 : 1 in 4x × 5x crosses. Therefore pentaploids crossed to tetraploids should favor gametes nearer n = 24 in transmission, whereas in crosses to hexaploids gametes nearer n = 36 would be favored. Overall extra chromosome loss when pentaploids were crossed to tetraploids and gain when crossed to hexaploids supports this hypothesis (Fig. 2).

Selection against gametes and zygotes with intermediate numbers of extra chromosomes could result in a platykurtic type of distribution that was observed in this study and a bimodal type where selection is severe enough. Only the 5x × 6x distribution approached what might be considered a bimodal type distribution (Fig. 2). Selection against the pentaploid level due to unfavorable endosperm genome ratios could also be the reason why the distributions of this study did not exhibit bimodality.

To conclude, it appears that extra chromosome transmission distributions are shaped by selection at both gametophytic and post-zygotic stages acting collectively. Post-zygotic selection, however may be influenced by two different mechanisms acting concurrently: 1) chromosome imbalance due to aneuploidy and/or 2) endosperm imbalance – maternal : paternal genome endosperm ratios deviating from 2 : 1. Table 6 gives various endosperm ratios expected when triploids and pentaploids are crossed in various combinations. Certain crosses with triploids would experience greater endosperm balance discrepancies (4 : 1) than would pentaploids (3 : 1). More importantly, such a mechanism could lead to differential transmission rates of extra genome chromosomes when oddploids are crossed to different ploidy levels, and to reciprocal differences as well.

Table 6. Endosperm maternal : paternal genome ratios for various crosses with triploids and pentaploids

Oddploid	Cross	Gamete chrom. no.		Endosperm ratio[b]	Deviation from 2 : 1
		♀	♂		
Triploid	3x × 2x	x	x	2 : 1	0
		2x	x	4 : 1	2
	2x × 3x	x	x	2 : 1	0
		x	2x	1 : 1	-1
	3x × 4x	x	2x	1 : 1	-1
		2x	2x	2 : 1	0
	4x × 3x	2x	x	4 : 1	2
		2x	2x	2 : 1	0
Pentaploid	5x × 4x	2x	2x	2 : 1	0
		3x	2x	3 : 1	1
	4x × 5x	2x	2x	2 : 1	0
		2x	3x	1.33 : 1	-0.67
	5x × 6x	2x	3x	1.33 : 1	-0.67
		3x	3x	2 : 1	0
	6x × 5x	3x	2x	3 : 1	1
		3x	3x	2 : 1	0

[a] Note: Gametes of the triploid vary from n = x to n = 2x, and those of the pentaploid from n = 2x to 3x

[b] Maternal/paternal genome

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