The population cytogenetics of *Crepis capillaris*.

II. The stability and inheritance of B-chromosomes

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Metacentric B-chromosomes in *Crepis capillaris* undergo somatic non-disjunction in the developing inflorescences. Non-disjunction occurs at several stages in development and is seen as differences in B-number (i) between pollen mother cells (PMCs) within florets, (ii) between florets within capitula, and (iii) between capitula within inflorescences. About half the plants studied showed variation in B-number within the inflorescence. The number of Bs in inflorescences is very variable but in most plants is greatly in excess of the zygotic number, ranging from 1.00 to 3.56 per PMC in 1B plants. Two rounds of non-disjunction occasionally occur in the same cell lineage. The inheritance of Bs is greatly enhanced over Mendelian expectation with average transmission of 0.90 through the pollen and 0.83 through the egg. The role of accumulation in the maintenance of the *C. capillaris* B-chromosome polymorphism is considered. Very strong selection pressures must operate against B-containing plants or gametes in natural populations.

INTRODUCTION

The only consistent features identifying B-chromosomes are that they are inessential for the survival of an individual and share no homology with regular members of the chromosome complement. Consequent on these characteristics, B-chromosomes often exhibit abnormal behaviour during division. Thus they may vary in number between cells and tissues within an individual and may even be excluded from whole organs as, for example, the roots of *Aegilops speltoides* and *Haplopappus gracilis* (Jones and Rees, 1982). Bs may also undergo directed non-disjunction at either meiotic or mitotic divisions which results ultimately in their numerical accumulation into gametes. Clearly the nature of any such accumulation mechanisms must be considered in assessments of the significance of B-chromosome polymorphisms in natural populations.

B-chromosomes have been reported from several localities in the widespread plant species *Crepis capillaris* (Abraham *et al.*, 1968; Rutishauser, 1960, 1963; Barthelmess and Bauchinger, 1962) and the stability and inheritance of these Bs has been described in plants derived from a Swiss population (Rutishauser, 1963; Rutishauser and

Rothlisberger, 1966; Rothlisberger, 1970). In the Swiss accession the Bs regularly undergo somatic non-disjunction in shoot meristems at the time of floral initiation with the result that the B-number in the flowers, and hence the germ-line, is increased. Bs thus experience enhanced transmission into the offspring over that expected from the original somatic number.

In British populations, B-chromosomes are a common feature of the genetic system of *C. capillaris* (Edgar, 1981; Whitehouse, 1981). Although the pattern of non-disjunction which has previously been described is also reflected in plants from British populations, there is a great deal of variation in B-behaviour. Indeed, in some plants no somatic accumulation occurs and thus B-inheritance corresponds to Mendelian expectations. In this paper we describe the distribution of B-chromosomes within plants of *C. capillaris* and B-behaviour at meiosis, and relate these observations to the transmission of B-chromosomes to the offspring.

MATERIALS AND METHODS

Both plants and achenes of *C. capillaris* were collected from B-containing populations at Bredon

Figure 1 Somatic chromosome complement of *Crepis capillaris* with a single metacentric B-chromosome. $2n = 6 + 1B^m$. Bar represents 5 μ m.

Hill, Hereford and Worcester (map reference SO 976407), and East Wretham Heath, Norfolk (TL 910886). Chromosome constitutions were determined from squash preparations of roots, leaves and bracts following colchicine treatment, fixation in 1:3 acetic alcohol, and Feulgen staining. For meiotic analyses, capitula were fixed in Carnoy and florets squashed individually in 2 per cent lacto propionic orcein. Crosses were made by rubbing capitula together without prior emasculation.

THE CHROMOSOME COMPLEMENT

The chromosome complement of *C. capillaris* consists of three pairs of individually-recognisable acrocentric chromosomes designated A, D and C in size order (Navashin, 1934). Chromosome D carries a nucleolar-organiser region on the short arm. The standard B-chromosome is a small metacentric element about two thirds the length of chromosome C of the basic complement (fig 1). C-banding shows that about 30 per cent of the B is heterochromatin located pericentromerically (Schweizer, 1973; Edgar, 1981). The B-chromosome from British populations is morphologically indistinguishable from the Swiss B of Rutishauser described by Schweizer (1973).

STABILITY OF B-CHROMOSOMES

(i) Roots, leaves and bracts

Several hundred plants of *C. capillaris* carrying B-chromosomes have been examined by standard root-tip analysis. In all these root-tip cells the

B-chromosome number shows constancy, both within- and between-roots and between sampling times. The mitotic behaviour of Bs in this organ then is as regular as that of the standard complement. Similarly, the B-content of young rosette leaves is constant and reflects accurately the B-composition of the roots of the same plant. Leaves from over 500 plants in natural populations have been sampled and no between-cell variation has been observed (Horton and Parker, unpublished). A more limited sample of the bracts carried on the developing flower scapes has been analysed and again the bracts maintain the B-number characteristic of leaves and roots. This result differs from the observations of Rutishauser and Rothlisberger (1966) who found a low frequency of 2B cells in bracts of plants with 1B in roots and leaves. Thus in this British material the B behaves in a regular, controlled fashion in the greater part of the plant.

(ii) Inflorescences

The behaviour of B-chromosomes during floral development has been assessed from the numbers of Bs in pollen mother cells (PMCs) of plants whose B constitutions were determined in root-tip cells. Three capitula (buds) from each plant and three florets from each of these capitula were examined at metaphase I of meiosis. B numbers were recorded in 40 PMCs from each of these nine florets per plant. In this study, variation in B number could be studied at a number of developmental levels: (i) between the inflorescence and the roots; (ii) between capitula within inflorescences; (iii) between florets within inflorescences; (iv) between PMCs within florets.

Figures 2—5 Metaphase I in PMCs of *Crepis capillaris* with different numbers of B-chromosomes. Figure 2. 0B. Figure 3. Single B^m univalent. Figure 4. B^m bivalent. Figure 5. Two B^m univalents. Bar represents 5 μ m.

Thirty-four plants were examined, eleven of which had no Bs in roots, eighteen had 1B and five had 2Bs. No B chromosomes were found in PMCs of plants which lacked Bs in the root-tip cells (fig. 2), confirming numerous other observations that the constitution of root-tip cells gives an exact test of the presence of Bs in a plant.

In the eighteen 1B plants, between PMC variation was found in only three florets out of the 162 examined. These had 0B+2B, 0B+4B, and 1B+2B, in each case with the lower number in excess. It cannot be established, however, at what stage this rare irregularity of disjunction takes place since all five anthers within the floret are joined into a tube and so were squashed together. The presence of 0B+4B PMCs, however, shows that not all the non-disjunction events leading to B variation are one-step.

Fifty-four capitula of 1B plants were examined and eleven (20 per cent) showed differences in B number between florets. At this level, the Bs show great heterogeneity in numbers. This is emphasised by the observation of nine different patterns in these eleven capitula involving 0B, 1B, 2B and 4B florets (table 1). The common pattern found was of two B-numbers in the three sampled florets of the capitulum, and only one capitulum had three different florets—2B, 4B, and a mixture of 0B and

4B PMCs. Only two combinations occurred twice—1B+1B+2B and 2B+4B+4B. In total, eight of the 18 plants showed between-floret variation in one or occasionally two capitula of the three sampled.

Variation within and between florets is reflected in differences of B distribution between capitula. Nine of the eighteen 1B plants showed variation at this level but only one plant gave any indication that non-disjunction may occur during the development of the inflorescence rather than during differentiation within capitula. In this single plant two capitula were uniform for 2B while in the third none of the florets had B-chromosomes. It is likely, however, that some of the variation which occurs by non-disjunction in development of capitula will not be detectable as a result of the high frequency of between-floret variation. For example, if non-disjunction gives rise to a 1B and a 2B capitulum, subsequent non-disjunction in florets of the 1B capitulum giving 2B florets will render the initial event undetectable.

Finally, we can compare the number of Bs in the inflorescence with that determined from the root tip cells. Nine plants had constant B numbers in their inflorescences: eight with 2B in all PMCs and the ninth uniformly 1B. Thus, although an increase in B number is the standard pattern, it is

Table 1 Different patterns of B-number distribution in inflorescences of plants of *Crepis capillaris* with 1B- and 2B-chromosomes in root-tip cells. B constitutions recorded in 40 PMCs from three florets in each of three capitula per plant

Somatic B number	Capitulum number									Mean B number	Total plants
	1			2			3				
1B	1	1	1	1	1	1	1	1	1	1.00	1
	0	0	0	2	2	2	2	2	2	1.33	1
	0	0	2	1/2	2	2	2	2	2	1.46	1
	1	1	1	1	2	2	2	2	2	1.56	1
	1	1	2	2	2	2	2	2	2	1.78	1
	0/2	2	2	2	2	2	2	2	2	1.86	1
	1	1	2	2	2	2	0/4	2	4	1.88	1
	2	2	2	2	2	2	2	2	2	2.00	8
	2	2	2	2	2	2	2	2	4	2.22	2
	2	4	4	2	4	4	4	4	4	3.56	1
											Total plants
2B	1	4	4	4	4	4	4	4	4	3.67	1
	2	4	4	4	4	4	4	4	4	3.78	1
	4	4	4	4	4	4	4	4	4	4.00	3
										Total plants	5

not universal and in some plants Bs must behave as regularly as the A complement. The nine plants exhibiting variable B numbers had PMCs with 0B, 1B, 2B and 4B chromosomes. No PMCs with 3Bs were found indicating that the doubling process affects all the Bs in the cell. In other studies PMCs with 3B chromosomes have been observed, albeit rarely (Edgar, 1981; Horton and Parker, unpublished).

The presence of 4B chromosomes in florets of four 1B plants indicates that a second round of non-disjunction sometimes takes place. This second non-disjunction event may occur at one of several developmental stages shown by variation between PMCs within florets, between florets, and possibly between capitula.

As a result of non-disjunction the average B frequency in PMCs of 1B plants is very variable. The mean frequency based on 360 PMCs per plant ranged from 1.00 up to 3.56 per PMC, with eight plants having a mean of 2.00. Overall the 18-plant sample averaged 1.94 Bs/PMC, just slightly less than double the somatic number determined in root tips. Clearly the transmission of Bs between generations should be greatly enhanced over Mendelian expectations although we would expect a high variance between individual crosses.

Five plants with 2B chromosomes in root-tip cells were examined in the same manner as the 1B plants. B-behaviour resembles that of 1B plants with two of the plants having variable B-numbers. Each carried a single floret with less than 4Bs in the PMCs (2B and 1B respectively). The maximum B-number observed in these plants was 4 with no

indication of the second round of non-disjunction found in 1B plants and the average B-frequency was 3.89 per PMC.

Two telocentric elements were recovered in a cross involving a standard metacentric B, presumably products of centric misdivision. At metaphase I in this plant PMCs uniformly had four Bs showing that non-disjunction is not dependent on the structure of the B chromosome.

METAPHASE I ASSOCIATION OF B-CHROMOSOMES

B-transmission will be influenced by the pairing and chiasma properties of Bs during meiosis. In particular, the presence of univalent Bs at metaphase-I (fig. 3) may lead to loss by lagging at later meiotic stages.

At metaphase I, the Bs of *C. capillaris* never associate with members of the standard A complement which is consistent with the general observation of lack of homology between As and Bs. When more than a single B is present the Bs may associate as bivalents or larger associations. The M-I association of B-chromosomes has been assessed in 26 plants with 2Bs in their PMCs, based on samples of 40 cells. The 2Bs usually form a bivalent; on average only 10 per cent of PMCs have a pair of B-univalents at metaphase I (figs. 4 and 5). The extent of B-univalence is variable, ranging between 30 per cent of cells in one plant and 0 per cent in three others (table 2).

Figures 6–8 Anaphase I in PMCs with B-chromosomes. Figure 6. Single B^m undergoing division. Figure 7. Centric misdivision of a B^m . Figure 8. 1:1 segregation of two B^m chromosomes. Bar represents 5 μ m.

Bivalents involving Bs appear normally chiasmate with one or perhaps two chiasmata which may be interstitial or distal, although the small size and extreme condensation of B bivalents precludes accurate assessment of chiasma frequency and position. It is also unclear whether univalent Bs exhibit any inter-arm pairing and chiasma formation at metaphase-I which would indicate that

the metacentric nature of the B reflects an isochromosomal origin. This has been suggested by Maluszynska and Schweizer (1989) from studies of the nucleolus-organiser properties of Swiss-derived Bs. Pachytene behaviour of Bs examined by SC spreading also reveals extensive inter-arm pairing (Jones *et al.*, in press).

Univalent B chromosomes show the usual pattern of abnormal segregations. Division of the B may occur at first or second anaphase with both chromosome and chromatid lagging, and rarely centric misdivision occurs (figs. 5–8). Some meiotic loss of B chromosomes, then, is likely when univalence occurs, reducing the gametic frequency of Bs.

The pattern of B-chromosome association showed no significant differences between the two widely separated populations.

Table 2 Patterns of association of B-chromosomes at metaphase I in plants with 2B and 4B chromosomes, based on 40 PMCs per plant

B number	Metaphase I associations					Total plants
	IV	III+I	2II	II	2I	
2B				40	0	3
				39	1	1
				38	2	5
				37	3	4
				36	4	2
				35	5	3
				34	6	1
				33	7	1
				31	9	2
				30	10	2
				28	12	1
				35.7	4.2	26
				89.4%	10.5%	
4B	40	0	0			6
	39	1	0			1
	38	2	0			1
	37	3	0			1
	36	3	1			1
	35	3	2			1
	34	5	1			1
	33	7	0			1
						1
						13
Totals	37.8	1.9	0.3			
	94.6%	4.6%	0.8%			

INHERITANCE OF B CHROMOSOMES

Due to the efficiency of the pre-meiotic accumulation mechanism, the B-chromosomes of *C. capillaris* are likely to be inherited with transmission rates higher than the expected 0.5 per B. Twelve reciprocal and two non-reciprocal crosses were carried out between 0B plants and those with a single B in root tip cells in order to determine transmission rates through both eggs and pollen of the same plant: 658 offspring were examined, 80 per cent of which had a single B, 2 per cent had two Bs and only one plant carried three Bs (table 3).

Overall, the transmission rate through the pollen was 0.90 per B (274 offspring) and through the

Table 3 Inheritance of B-chromosomes in *Crepis capillaris*. $\bar{k}$ = average transmission frequency per B

Cross number	0B♀ × 1B♂			$\bar{k}$	Total plants	1B♀ × 0B♂			$\bar{k}$	Total plants
	0	1	2			0	1	2		
1	8	16	1	0.72	25	7	18*	—	0.72	25
2	2	7	—	0.78	9	3	32	—	0.91	35
3	4	17	—	0.81	21	7	18	—	0.72	25
4	6	35	—	0.85	41	19	17	1	0.51	37
5	1	6	—	0.86	7	4	19	2	0.92	25
6	3	21	—	0.86	24	4	21	—	0.84	25
7	1	9	—	0.90	10	—	12	—	1.00	12
8	5	26	2	0.91	33	3	30	—	0.91	33
9	4	16	3	0.96	23	8	26	2	0.83	36
10	1	13	1	1.00	15	5	20	—	0.80	25
11	2	22	1**	1.00	25	2	10	—	0.83	12
12	—	40	1	1.03	41	4	31	1	0.92	36
13	—	—	—	—	—	5	12	—	0.71	17
14	—	—	—	—	—	2	39	—	0.95	41
Totals	37	228	9**	0.90	274	73	305*	6	0.83	384

* Includes 1 plant with telocentric misdivision products of the standard B.

** 1 plant with 3B.

egg 0.83 (384 offspring). These transmission rates are not significantly different ($\chi^2 = 5.34$ ns). The transmission rates varied from 0.72 to 1.025 per B through the pollen and 0.51 to 1.00 per B through the eggs (table 3). In general there was little difference between reciprocal crosses although in cross 4 the difference was highly significant (0.51 vs. 0.85 per B, $\chi^2 = 11.91^{***}$). Such a dramatic difference in reciprocal crosses probably results from variation in B numbers between capitula since crosses were not carried out using a single capitulum as both egg and pollen donor.

An attempt was also made to assess the extent of B-loss at meiosis, if any, by comparing the average B-content deduced from PMC B-numbers ("expected") with the average B-content of a

sample of the progeny of that plant ("observed"). Eight plants were tested in which the mean B number in PMCs ranged from 1.00 to 3.56 (table 4). B-transmission was once again greater than the 0.5 expected from Mendelian inheritance. The average transmission through the egg was 0.99 per B but the pollen transmission was only 0.68, largely as a result of three crosses with very low values.

In these eight crosses there was a general positive relationship between the expected and observed B numbers. Seven of the eight crosses, however, gave deficiencies of Bs in the offspring, some of which were large. Indeed in the two plants with the lowest PMC values (1.00 and 1.56; crosses four and eight in table 4) the deficits were greater than the observed B transmissions themselves. Five

Table 4 Observed and expected transmission of B-chromosomes in *Crepis capillaris*. The expected transmission values are calculated as 50 per cent of the average B constitution of PMCs in the nine florets sampled per plant (see Table 1)

Cross number	0B♀ × 1B♂			$\bar{k}$	Total plants	1B♀ × 0B♂			$\bar{k}$	Total plants	Observed transmission	Expected transmission
	0	1	2			0	1	2				
1	10	17	—	0.63	27	7	35	1	0.86	43	0.75	1.11
2	4	23	—	0.85	27	1	28	3	1.06	32	0.96	0.94
3	2	5	—	0.85	7	11	33	4	0.85	48	0.85	1.00
4	33	4	—	0.11	37	6	2	—	0.25	8	0.18	0.50
5	—	5	9	1.71	14	11	3	9	1.69	13	1.70	1.78
6	9	2	—	0.18	11	—	4	14	1.78	18	0.98	1.00
7	8	35	1	0.86	44	1	32	—	0.97	33	0.92	1.00
8	10	3	—	0.23	13	12	5	2	0.47	19	0.35	0.78
Totals	76	94	10	0.68	180	39	142	33	0.99	214		

of the eight crosses showed a close correspondence between observed and expected. Interestingly, the single plant in which two pre-meiotic B doublings had occurred transmitted an equally high B number through both pollen and eggs (1.70 per gamete; cross five).

A number of factors may have influenced these results. Firstly, in calculating average B transmission both egg and pollen side results were pooled. Secondly, the numbers of offspring scored in some of the crosses was rather small. Thirdly, as with the crosses reported above, different capitula were used for reciprocals. It is clear that in these plants, however, the deficit of Bs in some progenies is much greater than can be explained on the basis of univalent loss alone.

The general picture which emerges from these crosses is that B chromosomes in plants which initially carried only a single B are transmitted to their offspring greatly in excess of the expected 0.5 per gamete, generally with an enhancement of between 60 and 80 per cent. A small minority of plants, however, do show an overall loss of Bs, despite a pre-meiotic accumulation into the PMCs.

DISCUSSION

The developmental variation of B-number in *C. capillaris* was clearly demonstrated by Rutishauser and Rothlisberger (1966) in a line derived from a Swiss population. They showed that the stability of B-numbers observed in vegetative tissues breaks down when initiation of the flowering shoot begins. Indeed, the products of non-disjunction of a single B-chromosome—0B and 2B cells—were seen in shoot meristems about four days prior to the visible morphological changes associated with inflorescence initiation. The proportion of 2B cells in such 1B plants increased through development until over 80 per cent of the cells in older inflorescences carried two B-chromosomes. This predominance, they concluded, resulted from the faster rate of multiplication of 2B cells over both 1B and 0B. Similarly, 4B cells predominated in the inflorescences of somatically 2B plants, implying that 4B cells must outgrow cells with lower B-numbers. Such differences in growth rate remain untested in *C. capillaris*, but in the three species for which data are available, the mitotic cycle times are increased by the presence of Bs (Evans *et al.*, 1972). It would seem more likely, therefore that cells with enhanced B-numbers are at a positional advantage rather than a growth advantage; non-disjunction,

then, would be polarised with respect to the developing inflorescence.

No detailed analyses of B distribution in the inflorescences of *C. capillaris* have previously been made. Rutishauser and Rothlisberger (1966) reported only the proportions of cells with various numbers of Bs in particular tissues. It is not known how many cells or plants were involved in this assessment nor whether only PMCs were considered. The study of Brown and Jones (1976) using the Swiss B-line again indicates that some somatic doubling occurs in the development of the inflorescence but the extent of variation in this process cannot be deduced.

In the present analysis of B-chromosomes from British populations we have shown that non-disjunction events do indeed occur during inflorescence development in *C. capillaris*. It is clear from the method of analysis employed here that differences between germ-line cells can arise at various developmental stages, certainly as late as the differentiation of anthers within florets. As a result, the inflorescences of many plants carrying B-chromosomes are mosaics with PMCs having varying B-numbers. This mosaicism will inevitably result in a wider spectrum of B-numbers in the gametes, and hence zygotes, than would be the case in the absence of variation.

Despite the extensive non-disjunction of Bs in *C. capillaris* a plant was found in which the somatic and germ-line numbers were the same. Non-disjunction is not an invariable quality of the B-system, but it is not yet known whether this lack of variation is dependant on the B-genotype, the A-genotype or the A/B interaction. If the A-genotype is implicated then this would suggest that the behaviour of the B-system could be modified by selection. In other systems it has been shown that A-chromosome variation can influence B-behaviour. In *Hypochoeris maculata* the rate of transmission of a small telocentric B-chromosome through the egg is a heritable phenotype (Parker *et al.*, 1982 and unpublished). In maize, also, non-disjunction of the B is strain-dependent (Carlson, 1969).

There has been considerable interest recently in whether Bs in some species can be considered as parasitic elements (R. N. Jones in Cavalier-Smith, 1985). Clearly if the self-propagation of the B is subject to A-control this must influence our views of this contention, allowing as it does the possibility of selection of B-tolerant or non-tolerant autosomal genotypes. Recently, Nur and Brett (1985, 1987, 1988) have elegantly demonstrated that in the mealy bug *Pseudococcus affinis*

there are genotypes which affect the rate of transmission of B-chromosomes. Results of controlled crosses can be interpreted by a simple two-locus model in which the alleles affect condensation of the B-chromosomes which in turn affects the position adopted by the B on the metaphase plate and its subsequent segregation. Populations from which the laboratory lines were derived were polymorphic for these "transmission-reducing genotypes". Nur and Brett (1987) conclude that there is no B-heterogeneity affecting transmission characteristics in this species.

In the plants studied by Brown and Jones (1976), derived from Rutishauser's Swiss material, the Bs showed considerable irregularity in metaphase I association. In 2B PMCs, for example, only 60 per cent had a B-bivalent while in 4B PMCs the maximal quadrivalent was attained in only two-thirds of cells. This is in marked contrast to the values of 90 and 95 per cent respectively in the present sample. Clearly, B loss due to lagging at anaphase I and anaphase II will be much higher in the former sample. In the light of the studies of Nur and Brett (1987) studies of A-chromosome effects on transmission of *Crepis* Bs should be undertaken.

The high pairing efficiency of *C. capillaris* Bs may be a reflection of their isochromosomal origin. Maluzynska and Schweizer (1989) have demonstrated symmetry in the metacentric B with respect to a nucleolus-organiser region carried distally on each arm. The NOR was detected both by *in situ* hybridisation of biotinylated rDNA and by silver staining of NOR-associated proteins which indicates that these NORs are active in somatic cells. Further evidence for an isochromosomal origin of the *Crepis* metacentric B comes from zygotene and pachytene observations of surface-spread synaptonemal complexes in PMCs. In cells with a single B hairpin loops are frequently seen, indicating complete inter-arm homology (Jones *et al.*, in press). In cells with a pair of identical B-chromosomes resulting from non-disjunction, the two Bs are frequently paired together at zygotene and pachytene, though inter-arm pairing occurs in this situation too. The maintenance of B-associations through to metaphase I then requires regularity of inter-chromosomal chiasma formation within the B-bivalent.

The B-transmission values presented here indicate that in natural or indeed artificial populations of *C. capillaris* there should be a massive increase in B-frequency every generation of about 60–80 per cent. This does not seem to be the case in British populations which have relatively low B-

frequencies which appear to remain constant between generations (Edgar, 1981; Whitehouse, 1981). It is necessary, therefore, for there to be a compensating decline in B-numbers within a population to maintain the equilibrium, assuming B-accumulation by non-disjunction is indeed a feature of natural populations. In the mottled grasshopper *Myrmeleotettix maculatus*, in which accumulation of Bs occurs through directed segregation in oocytes (Hewitt, 1976), Robinson and Hewitt (1976) have demonstrated a cyclical change in B-frequency in natural populations. Increase occurs between adult and zygote, with a subsequent decline to adult levels of the previous generation by embryo mortality during the winter. The pattern of B-behaviour during the life-cycle of *C. capillaris* in natural populations will be reported in a later paper.

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