The population cytogenetics of *Crepis capillaris*.

III. B-chromosome effects on meiosis

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The B-chromosomes of *Crepis capillaris*, $2n = 6$, modify the pattern of chiasma formation in PMCs. With increasing B number, mean chiasma frequency increases in a linear fashion. The between-PMC variance for chiasma number also increases independently of the mean. All three bivalents increase in chiasma frequency in the presence of Bs but the smaller bivalents D and C increase disproportionately with respect to length. The "additional" chiasmata are predominantly distal in the long arms, with a decline in short arm and proximal long-arm regions. The chiasma effects of Bs are observed in comparisons between plants growing in natural populations, between plants in segregating families, and between PMCs within plants. B-chromosomes in this species markedly change the pattern of recombination in the genome.

INTRODUCTION

In many outbreeding plant species, B-chromosomes are a feature of the genetic system (Jones and Rees, 1982). Amongst the many facets of growth and development affected by the presence of B-chromosomes, considerable attention has been paid to crossing-over and chiasma formation at meiosis. Patterns of response to Bs are extremely diverse and a catalogue of effects has been recorded. In some species chiasma control is B-independent, in others Bs may increase or decrease chiasma number or alter patterns of chiasma distribution (Jones and Rees, 1982). Many authors have thus suggested that Bs, by serving as regulators of recombination during meiosis, may control the generation of genotypic, and hence phenotypic, variation in natural populations. An alternative view is that the B-effects on meiosis are non-adaptive and are simply a consequence of the addition of chromatin to the nucleus.

Natural populations of the plant *Crepis capillaris* (Compositae) are highly variable in their patterns of chiasma formation. Significant differences in mean cell chiasma frequency have been found between populations, between families within populations, and between plants within families (Whitehouse *et al.*, 1981). The mean PMC chiasma frequency ranged from 3.13 to 7.38 in different

plants, the lower chiasma score reflecting regular formation of a single chiasma in each bivalent of this three-bivalent species. In addition, although chiasmata tend to occupy characteristic positions in bivalents, there is marked positional chiasma variation of a quantitative nature. This study indicated a high level of allelic diversity in the genes controlling chiasma formation in standard plants drawn from natural populations of this outbreeding species.

In *C. capillaris*, plants with metacentric B-chromosomes were frequently encountered during the study of chiasma variation. The B-chromosomes themselves had distinctive effects on chiasma frequency and distribution in the A-complement and hence plants with Bs were excluded from that investigation (Whitehouse *et al.*, 1981). The only previous study of chiasma effects of *Crepis* Bs has been that of Brown and Jones (1976) who studied experimental material derived from the Swiss line of Rutishauser (1960, 1963). It is clear that the chiasma effects of Bs derived from British populations presented here differ strikingly from those of the Swiss Bs. In addition two geographically and ecologically distinct British populations have been studied allowing an assessment to be made of variation in patterns of chiasma response to B-chromosomes. The transmission behaviour of *C. capillaris* Bs derived

from these populations has previously been reported and this indicated only slight interpopulation differences (Parker *et al.*, 1989). *C. capillaris* is particularly suitable for studies of chiasma effects since it has only three bivalents and these are individually recognisable. This allows finer discrimination of B-effects on chiasmata than is possible in most organisms.

MATERIALS AND METHODS

(i) Materials

Ripe achenes and mature plants were collected from natural populations at East Wretham Heath, Norfolk (O.S. 571288; EWH) and on Bredon Hill, near Elmley Castle, Worcestershire (O.S. 973408; BH) over the period 1976–79. A further generation was raised by intercrossing population plants. Plants were maintained in experimental glass-houses at the University of Birmingham and Queen Mary College Field Station in Essex.

Capitula containing florets at the appropriate meiotic stage were collected from the plants when available and immediately fixed in Carnoy's fixative (6:3:1) overnight at room temperature and stored at -10°C .

(ii) Cytological technique and scoring procedure

Florets at metaphase-I were squashed in 2 per cent lactopropionic orcein and chiasmata were scored in 40 pollen mother cells (PMCs) per plant. The chromosome complement of *C. capillaris* consists of three chromosomes, designated A, D and C by Navashin (1925), which may be identified at both mitosis and meiosis on the basis of length and centromere position (Tease and Jones, 1976). At metaphase-I of meiosis, the three chromosomes of the complement can be subdivided into 11 regions of approximately equal length and chiasmata can be ascribed to these regions (see fig. 1).

RESULTS

The effects of B-chromosomes on chiasma conditions in the standard chromosome complement of *C. capillaris* may be assessed in a variety of situations. Chiasma variation between individuals which have grown to maturity in B-containing natural populations may reflect B-chromosome effects, the effects of background genotype or

Figure 1 Diagrammatic representation of the karyotype of *Crepis capillaris* $2n=6$ with the subdivisions used for defining chiasma location. SA=shortarm; P, I, D=proximal, interstitial and distal.

environmental influences on chiasmata. These effects are likely to be confounded, and it may therefore be difficult or impossible to establish specific B-chromosome effects in this situation.

By contrast, genotypic effects can be identified in plants grown from seed to maturity under a common environmental regime. In the present study the offspring of single-pair crosses segregating for the presence or absence of B-chromosomes have been studied. In these crosses the average background genotypic effects on chiasma formation should be similar in the two groups of full-sibs which differ solely in respect of B-chromosomes.

The effects of B-chromosomes on chiasma conditions in the A-chromosomes can be investigated directly in individuals which show instability of B-distribution during the development of the inflorescence (Parker *et al.*, 1989). In these plants, different B-numbers can be assessed against a common A-chromosome background genotype.

1. Chiasma frequency per PMC

Family 1 derived from a cross between a plant from East Wretham Heath with a single B^m in somatic tissues as egg parent and a standard 0B plant as pollen parent, consisted of 20 full sibs, ten of which carried a single metacentric B-chromosome in somatic tissues. As a result of non-disjunction during inflorescence development, however, plants derived from embryos with a single B usually carry two B-chromosomes in their PMCs (Parker *et al.*, 1989). Only florets with two Bs were scored for chiasma frequency (fig. 2)

In this family, mean chiasma frequency ranged from 3.025 to 4.857 per PMC, with an overall mean of 3.905 (table 1). The two groups defined on the basis of B-content, however, were clearly distinct. The 0B plants had a mean chiasma frequency of

Figure 2 (a) Chromosome complement of *Crepis capillaris* with a single metacentric B-chromosome; $2n = 6 + 1B^m$. (b) Somatic complement with two telocentric B-chromosomes resulting from fission of a B^m ; $2n = 6 + 2B^t$. (c) Metaphase-I PMC with a B^m -chromosome bivalent; five chiasmata in the three autosomal bivalents. (d) Metaphase-I PMC with an association of four B^m -chromosomes (arrowed); seven chiasmata in the autosomal bivalents. Bar represents 5 μ m.

3.42 and all ten plants had mean frequencies below 4.00 chiasmata per PMC. All the B-containing plants, by contrast, had mean chiasma frequencies above 4.00 with an overall mean of 4.39. The ranges of these full-sib groups thus showed no overlap and the difference in means was 0.97 per PMC, an increase of 28 per cent in B-containing plants. In this family, then, the presence of two Bs in PMCs leads to an increase of roughly one chiasma in the A-complement over full sibs without Bs.

Two families (2 and 3) from Bredon Hill with a wider range of B-numbers have also been analysed (table 2). Both families were derived from crosses between 1B and 0B plants as egg and pollen parents respectively, but two rounds of non-disjunction occurred in the development of some florets giving up to 4Bs in the PMCs of some offspring. Thus in these families four floret types were analysed with the following B-constitutions—0B, 1B, 2B and 4B. Again, a clear relationship between B-number and mean chiasma frequency was observed. Florets with 2Bs in PMCs have 0.90 and 0.94 more chiasmata than their 0B sibs, very similar to the difference shown in Family 1. 1B

florets show approximately half this difference, 0.48 “extra” chiasmata in both families. The effect of 4Bs is slightly more than twice the 2B value, with an increase of 2.35 and 2.63 in families 2 and 3 respectively. Thus the chiasma frequency increase with increasing numbers of Bs is roughly linear and there is no indication of a threshold level in B-effect of the kind noted in *Myrmeleotettix maculatus* (Hewitt and John, 1967). The differences in chiasma frequency between B-chromosome classes were found to be significant in both families ($VR = 3.3$; $P < 0.05$ and $VR = 7.78$; $P < 0.01$ respectively; table 3).

The B-effect on chiasma frequency appears to be independent of the number of B-bodies present in a PMC but dependent on the amount of B-chromatin. Thus telocentric Bs (B^t) derived from a standard B^m by centric misdivision in an experimental cross, have standard chiasma frequency effects: plants with $2B^t$ in PMCs (equivalent to $1B^m$) have 0.36 more chiasmata than 0B full sibs while those with $4B^t$ (equivalent to $2B^m$) have 1.03 more chiasmata per PMC (table 4; fig. 2). The quantity of B-material is significant in the generation of this chiasma effect, rather than B-number.

Table 1 Mean chiasma frequencies per PMC of the three bivalents A, D and C, and between-PMC variances, expressed as the square root, in a family segregating for B-chromosomes in *Crepis capillaris*. Ten plants with 0B in PMCs and ten with 2B were studied, 40 PMCs per plant. The cross involved plants from the EWH population

PMC B-Number	Plant No.	Mean Chiasma Frequencies				$\sqrt{S^2}$
		A	D	C	Total	
0B	1	1.025	1.00	1.00	3.025	0.3202
	2	1.075	1.00	1.00	3.075	0.3273
	3	1.175	1.05	1.00	3.225	0.3434
	4	1.225	1.025	1.00	3.25	0.3453
	5	1.20	1.10	1.00	3.30	0.3630
	6	1.30	1.00	1.05	3.35	0.3655
	7	1.525	1.05	1.00	3.575	0.3536
	8	1.575	1.00	1.025	3.60	0.3530
	9	1.80	1.075	1.00	3.875	0.3486
	10	1.825	1.075	1.025	3.925	0.3572
	Means	1.37	1.04	1.01	3.42	0.3477
2B	1	1.65	1.375	1.125	4.15	0.4055
	2	1.625	1.375	1.20	4.20	0.4157
	3	1.65	1.45	1.15	4.25	0.4190
	4	1.60	1.45	1.25	4.30	0.3903
	5	1.575	1.60	1.20	4.375	0.3934
	6	1.775	1.525	1.10	4.40	0.3742
	7	1.80	1.40	1.275	4.475	0.4082
	8	1.80	1.525	1.20	4.525	0.4019
	9	1.90	1.525	1.125	4.55	0.3952
	10	1.727	1.95	1.18	4.857	0.3888
	Means	1.71	1.50	1.18	4.408	0.3992

Table 2 Mean PMC chiasma frequencies of florets with different numbers of B-chromosomes in two experimental families of *Crepis capillaris*. Five florets and 40 PMCs per floret were scored in each B-class. Both families were derived from the BH population

Family	Mean chiasma frequency			
	0B	1B	2B	4B
2	3.78	4.25	4.73	6.13
3	3.75	4.23	4.65	6.37

Table 3 Analysis of variance of mean chiasma frequency in florets with different numbers of B-chromosomes in *Crepis capillaris*. The B-chromosomes were derived from the BH population

Item	df	SS	MS	VR	P
Between B-class	3	9.388	3.129	7.784	<0.01
Within B-class	16	6.426	0.402		
Total	19	15.814			

B-chromosomes vary in number between PMCs within florets, between florets within capitula, and between capitula within inflorescences (Parker *et al.*, 1989). Three plants exhibiting extensive number variation have been examined for chiasma

Table 4 Chiasma frequencies in a family segregating for telocentric B-chromosomes of *Crepis capillaris*. Five individuals in each B¹-class were scored, 40 PMCs per plant

	PMC B-constitution		
	0B	2B ¹	4B ¹
Mean chiasma freq.	3.72	4.08	4.75
Range	3.63–3.85	3.88–4.30	4.48–5.25

frequency in PMCs. In all three, the mean number of chiasmata per PMC increased from 0B to 2B and/or 4B as in the full sib families. Due to small sample sizes, however, the increase was not significant in two of these plants. In the third, 1B and 2B showed significant increases of 0.69 and 1.30 respectively over 0B PMCs. The B-effect demonstrated between full sibs, then, is reproduced against a common background genotype.

Is the chiasma-enhancing B-effect, shown between PMCs within plants and between full-sibs, also demonstrable in plants flowering in the wild in polymorphic populations, whose genetic relationships are unknown? Two factors could obscure any B-effects: the extensive genetic variation for chiasma frequency of the A-set in natural

populations, and environmental effects on chiasma formation. Despite this the results are clear: in both populations the presence of Bs is associated with an enhanced chiasma frequency. At EWH for example 1B plants have 0.76 more chiasmata per PMC than 0B plants, and all six 1B plants in a sample of 30 fall within the top ten ranked chiasma scores. This pattern was repeated in five of a further six polymorphic populations examined. Population B-frequency, however, does not correlate with mean population chiasma frequency which presumably reflects the high level of chiasma frequency variation which is unconnected to presence vs. absence of Bs.

2. Between-PMC variance

A common effect of B-chromosomes, in a variety of species, is that between-PMC variance increases independently of any increase in mean chiasma frequency (Jones and Rees, 1967). In *C. capillaris*, increased between-PMC variance is observed in B-containing PMCs but as we have seen there is also a rise in mean chiasma frequency. Are these two events separable, or does the magnitude of the variance simply reflect the mean?

In the segregating family 1, the between-PMC variance (transformed as the square root) shows no significant regression with mean chiasma frequency in either the 0B or 1B plants (table 1). The variances of the two groups show no overlap, ranging from 0.3202–0.3655 in 0B plants and 0.3888–0.4190 in 1B plants (table 1). The enhanced variance of B-containing plants is shown in all experimental families and also characterises buds collected from plants growing in natural populations. Thus mean chiasma frequency and between-PMC variance respond independently to the presence of Bs in this species.

3. Bivalent chiasma frequency and chiasma location

a. Bivalent chiasma frequency

In *C. capillaris* the three bivalents are individually recognisable. Thus the chiasma increase due to the presence of Bs can be partitioned between bivalents and, at a finer level of discrimination, between regions within bivalents (fig. 1).

In the segregating families, the response of bivalents to the presence of Bs is rather variable (table 1). However, in all cases the greatest percentage increase is shown by bivalent D, the nucleolus-organiser chromosome, which in most

cases accounts for about 50 per cent of the total increase, at least in 0B/2B comparisons. Bivalents A and C are more variable in their response. In general, bivalent C increases more than A but the pattern is reversed in some families. Presumably background genotype influences the distribution of "extra" chiasmata between bivalents. The preferential formation of additional chiasmata by bivalent D is shown by both the EWH- and BH-derived B-chromosomes, again indicating the similarity of the effects of these Bs.

In standard 0B plants of *C. capillaris*, chiasma frequency per bivalent is directly proportional to bivalent length. In the presence of B-chromosomes, however, this relationship largely disappears and in some families mean chiasma frequencies of all three bivalents are very similar in PMCs with two B-chromosomes.

b. Chiasma location within bivalents

In standard 0B plants, certain regions of each chromosome are preferentially-favoured for chiasma formation while others are chiasma deficient. This is particularly marked in bivalent D where the chiasmata are often preferentially-localised in the proximal third of the long arm. In bivalent A chiasmata are most frequent in the short-arm and in the distal region of the long arm, while in the C chromosome short-arm and proximal long-arm chiasmata predominate. In the previous analysis of chiasma variation in *C. capillaris* this was manifested by the high significance of the term "regions within chromosomes" in the analysis of variance (Whitehouse *et al.*, 1981). However, extensive variation in chiasma distribution patterns was evident from the significance of the interaction terms at the levels of populations, families and plants within families. Individual variation in bivalents A and C was largely responsible for these results.

Chiasma distribution in B-containing individuals is likely to be modified simply as a result of the increase in chiasma frequency. Thus changes from rod to ring bivalents may increase the proportion of chiasmata present in short arms. The B-effects on chiasma distribution observed in *C. capillaris* are more complex than this, however, and are to some extent population-dependent.

In the BH plants the three bivalents show individual responses to the presence of 2Bs. In bivalent A, the short arm chiasmata decline in number while the three regions of the long arm increase more or less equally. In bivalent D, the chiasma increase of about 50 per cent is accom-

plished by a slight decline in the numbers of proximal chiasmata and a massive increase in distal chiasmata. In bivalent C, chiasma frequency remains constant in the short arm but increases four-fold in the distal segment of the long arm (table 5). In the Bredon Hill population, then, a common trend is apparent: chiasma increase is shown predominantly by distal regions of the long arms; short arms or proximal long arm regions are either unaffected or even show a slight decline in chiasma frequency. This behaviour is clearly differential with respect to chromosome region and is not simply dependent on the chiasma frequency of these regions in standard 0B plants. Only three of the eleven regions in 0B plants have chiasma frequencies higher than 0.5 and only one (proximal segment of D) reaches 0.75.

The results from the East Wretham Heath population show a similar pattern (table 6). The increase in chiasma frequency in distal regions however is accompanied by a decline in the short arms and proximal regions of the long arms. This can be illustrated by considering chiasma distribution only in monochiasmate bivalents in 0B and 2B PMCs which eliminates any influence of changes in mean bivalent chiasma frequency. In bivalent A, short arm and proximal long arm regions decline from a joint chiasma frequency of 0.36 in 0B PMCs to only 0.04 in 2B PMCs. In bivalent D, the extreme localisation in the proximal legion of the long arm (0.9 chiasmata per PMC) breaks down, with the majority of chiasmata (0.6 per PMC) now interstitial and only 0.2 proximal. The distal movement is similarly

Table 5 Chiasma frequency per cell in plants with different numbers of B-chromosomes from the BH population. Chiasmata have been allocated to 11 regions on the three bivalents (see fig. 1). Four plants were scored in each B-class, 40 PMCs in each. (SA = short arm; P, I, D = proximal, interstitial and distal regions of the long arm)

Bivalent	B number	Chiasma position and frequency				Mean chiasma frequency
		SA	P	I	D	
A	0	0.37	0.46	0.28	0.64	1.75
	1	0.36	0.63	0.20	0.66	1.85
	2	0.18	0.59	0.45	0.77	1.99
	4	0.25	0.96	0.15	0.95	2.31
D	0	0.02	0.75	0.19	0.19	1.33
	1	0.01	0.84	0.06	0.41	1.44
	2	0.07	0.66	0.35	0.65	1.73
	4	0.13	0.91	0.04	0.96	2.04
C	0	0.55	0.45	—	0.15	1.05
	1	0.49	0.39	—	0.19	1.07
	2	0.47	0.50	—	0.71	1.68
	4	0.46	0.50	—	0.94	1.90

Table 6 Chiasma distribution in the segregating family of *Crepis capillaris* from EWH with 0B or 2B in their florets (see table 1). Chiasmata have been allocated to the 11 regions on the three bivalents. Bivalents with 1 and 2 chiasmata have been presented separately. The figures are given as percentages, and those in parenthesis are small samples (less than 10 observations). A total of 800 PMCs were scored

		Chiasma distribution (percentage)								
Bivalent	PMC B-number	1 chiasma				2 chiasmata				Mean chiasma frequency
		SA	P	I	D	SA	P	I	D	
A	0B	5	31	43	21	40	6	20	35	1.37
	2B	0	4	87	9	2	12	42	44	1.71
D	0B	<1	91	4	5	(0	50	6	44)	1.04
	2B	1	23	57	19	<1	30	30	40	1.50
C	0B	43	49	—	8	(50	0	—	50)	1.01
	2B	11	52	—	37	28	23	—	49	1.18

shown by bivalent C. A roughly equal short arm: proximal region of long arm distribution in 0B PMCs is replaced by a long arm proximal/distal equality in 2B PMCs.

A similar pattern of chiasma redistribution is demonstrable for bichiasmate A bivalents. Particularly striking is the decline from 0.4 to only 0.02 in short-arm chiasmata in the presence of two B-chromosomes. Thus most bichiasmate A bivalents in 0B PMCs are rings with a short arm + interstitial/distal chiasma distribution, but in 2B PMCs the majority are rods with interstitial + distal chiasmata.

DISCUSSION

The presence of B-chromosomes in *C. capillaris* results in, or is accompanied by, modification of the pattern of chiasma formation in the A-chromosomes.

A number of changes have been established:

- (i) mean chiasma frequency per PMC increases with increasing number of B-chromosomes;
- (ii) the between-PMC variance in chiasma number increases, independently of the mean;
- (iii) all three bivalents may show increases in chiasma frequency in the presence of B-chromosomes but in bivalents D and C increase is disproportionately large with respect to length;
- (iv) "additional" chiasmata form predominantly in the distal regions of the long arms of bivalents D and C;
- (v) in the EWH population chiasmata decrease markedly in the short arms and proximal regions of the long arms of all bivalents in 2B PMCs, while in BH plants the number of chiasmata in these regions is maintained or shows only a slight decline.

B-chromosome effects on chiasma formation in *C. capillaris* have previously been demonstrated by Brown and Jones (1976) using an experimental population maintained for about 15 generations in culture, with the Bs originally derived from a Swiss population (Rutishauser, 1960). The Swiss and British Bs are both metacentric and about one third the length of the smallest standard bivalent (C). Maluzynska and Schweizer (1989) conclude that the Swiss B is an isochromosome on the basis of staining and *in situ* hybridisation of rDNA. The B apparently carries active nucleolar-organiser regions stainable by silver distal on each arm. Using the same silver staining method we have been unable to demonstrate these regions in Bs

from Bredon Hill (Jones *et al.*, 1989). However, studies of chromosome pairing at zygotene and pachytene by synaptonemal complex spreading show a very high frequency of inter-arm association in both single Bs and 2Bs thus demonstrating extensive arm-homology and a presumptive origin by isochromosome formation (Jones *et al.*, 1989).

The British and Swiss Bs, then, show morphological similarity but perhaps not complete identity. In B-behaviour also, small differences can be detected between the accessions. Both undergo directed non-disjunction during the development of the inflorescences (Parker *et al.*, 1989), but B-association at metaphase-I is much lower in Swiss Bs than in British Bs (Brown and Jones, 1976; Parker *et al.*, 1989).

It is perhaps not surprising, then, that the earlier findings by Brown and Jones (1976) are at variance with those presented here in many details of chiasma behaviour although this is true of both the standard A-complement and B-behaviour. Brown and Jones (1976) report that in standard 0B plants there is no simple chromosome length-chiasma frequency relationship, with the C bivalent regularly forming two chiasmata and hence having a higher mean chiasma frequency than the larger D bivalent. This contrasts with the linear relationship demonstrated here and found in all comparable studies (Richardson, 1935; Tease and Jones, 1976; Whitehouse *et al.*, 1981). In terms of B-effects, the studies agree that the between-PMC variance increases in the presence of Bs and that there is an overall rise in chiasma frequency. However, Brown and Jones found that this increase affected all bivalents equally, whereas in the present study, the bivalents reacted differentially to the presence of Bs.

It has been suggested that those species in which Bs induce an increase in chiasma frequency do so by lengthening the time of effective meiotic pairing (Barlow and Vosa, 1970; Rhoades and Dempsey, 1972) or by increasing the number of sites available for chiasma formation. No data are available on meiotic timing in B-systems, but the Bs of *C. capillaris* have recently been shown to have a striking effect on synaptonemal complex length which may well be significant here. In 2B PMCs, the total SC length of the A complement is increased by about 50 per cent (Jones *et al.*, 1989). If chiasma frequency is dependent on the amount of effective pairing as revealed by the SCs, then the B-dependent chiasma effect may be epistatic to this underlying process. The regional differences in B-effect, similarly, may reflect

differential SC length increases within and between chromosome arms. What is very striking about B-effects on chiasma distribution is that chiasmata form closer together in the interstitial/distal regions of the long arms than in standard OB plants. Thus Bs apparently modify interference between potential sites of chiasma formation, but this may also be interpreted as an increase in the number or availability of sites for chiasma formation.

The effects of B-chromosomes on the frequency and distribution of chiasmata in *C. capillaris* are PMC-specific. Clearly Bs act on each PMC independently and directly to control chiasma formation, rather than indirectly via a metabolic modification of all PMCs. This argues for direct, mechanical involvement of Bs in chiasma control. PMC-specificity for chiasma frequency has also been reported in mosaics of *Gibasis linearis* (Brandham and Bhattarai, 1977) and the grasshopper *Myrmeleotettix maculatus* (Hewitt and John, 1967). In this study, two geographically- and ecologically-distinct populations of *C. capillaris* have been examined. Although the results are very similar, some differences have been noted, in particular the influence of Bs on chiasma distribution. This indicates a certain amount of genotypic diversity in control of this feature. In the previous study of B-inheritance in this species (Parker *et al.*, 1989) genotypic variation was again evident, although this was intra- rather than inter-populational. The source of this variation is not yet known but may reflect B-chromosome diversity. As mentioned above, the Swiss and British Bs are somewhat divergent and subtle evolutionary changes may also have occurred in the EWH and BH lineages.

The influence of B-chromosomes on the progress of meiosis has significant genetic consequences in terms of crossing-over. Most intriguing is the modification of within-bivalent chiasma distribution. Despite the higher chiasma frequency of B-containing PMCs, large sections of the genome such as the short-arms are relatively sheltered from recombination. By contrast distal regions of the long arms undergo greatly enhanced levels of recombination. The Bs of *Crepis*, then, will lead to a modification of the gametic spectrum and hence the zygotic spectrum in natural populations. It is not clear in any organism, however, whether alteration of the chiasma pattern has any selective consequences in either natural or experimental populations. The high heritability of chiasma frequency demonstrated in *Schistocerca* (Shaw, 1972) and *Hypochoeris* (Parker, unpublished) argues for low fitness for this character.

Modification of chiasma distribution by B-chromosomes has been reported in a number of species of plants and animals (*Naias marina*, Viinikka, 1973; *Puschkinia libanotica*, Barlow and Vosa, 1970; *Tettigidea lateralis*, Fontana and Vickery, 1973; *Zea mays*, Ward 1976). It would be instructive to study pairing pattern modification in standard and B-containing individuals of some of these organisms to establish whether increases in SC length always accompany Bs. Such studies may well give us novel insights into the normal processes of synapsis and recombination during meiotic prophase.

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