B-Chromosome Systems
in the Pocket Mouse, *Perognathus baileyi*:
Meiosis and C-Band Studies

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Abstract. The heterochromatin characteristics and meiotic behavior of the B-chromosome system of the pocket mouse, *Perognathus baileyi*, are described. B-chromosomes are associated both with a meiotic accumulation mechanism and with an increase in average chiasma frequency in the A-chromosome set in males. Three morphological classes of B-chromosomes are recognizable, and the mechanisms of origin of each are discussed.

Introduction

Supernumerary, or B-chromosomes, have now been described for a dozen or so species of mammals, including marsupials (Hayman and Martin, 1965; Hayman et al., 1969), carnivores (Gustavsson and Sundt, 1965), and many rodents (*Rattus,* Yong and Dhaliwal, 1972; Gropp et al., 1970; Wahrman and Gourevitz, 1973; *Sigmodon,* Zimmerman, 1970; *Apodemus,* Hayata, 1973; *Reithrodontomys,* Shellhammer, 1969; and *Perognathus,* Patton, 1972). Despite knowledge of a broad range of taxa in which B-chromosomes are known to occur, little other information on these systems is available. Few studies have addressed questions related to the cytogenetic characteristics of mammalian B-chromosome systems (such as meiotic behavior, heterochromatin content, DNA characterization, and so forth). Not surprisingly, therefore, no work has as yet been published on populational attributes or consequences of such systems (for example, temporal variation and effect on individual fitness). The present paper examines some of the cytogenetic features of the complex system of B-chromosomes described earlier for the pocket mouse, *Perognathus baileyi* (Patton, 1972); in particular, details of heterochromatin content and meiotic behavior. A companion paper (Patton, Ms) discusses in greater detail aspects of both geographic and temporal variation in B-chromosomes in the species in the context of the origin, spread, and present-day populational characteristics of the system. A third paper (Patton and Yang, ms) deals with the relationship between B-chromosomes and both individual and populational morphometric and genic variability parameters.

Materials and Methods

One hundred and ten specimens of *P. baileyi* from five populations from Arizona in the United States and Sonora and Baja California Norte in Mexico were used in this study. These specimens are in addition to the more than 200 individuals examined subsequent to the earlier report on the species (Patton, 1972).

C-metaphase preparations were made from bone marrow cells by the in vivo colchicine-hypotonic citrate sequence described previously (Patton, 1967). Flame or air-dried slides were stained in standard 10% Giemsa for gross chromosomal determinations while air-dried slides alone were used for C-banding. The latter was accomplished by pretreatment of thoroughly dried slides in 0.1 N HCl for 10 min followed by 2 to 4 min treatment in $2 \times SSC$, pH 12.4, and an overnight incubation in $2 \times SSC$ at 65° C. Slides were stained in 1% Giemsa for 10 min. This is a slight modification of the general C-band technique (Cooper and Hsu, 1972). Both standard and C-band staining were preformed on slides from each of the 110 specimens examined.

Meiotic preparations were made from 33 males from two populations by a testicular air-dried technique similar to that used by Stock et al. (1972). C-banding of meiotic figures was performed as with bone marrow mitoses.

All specimens examined are catalogued as standard skin with skull museum voucher specimens in the mammal collections of the Museum of Vertebrate Zoology. Locality information and respective sample sizes are as follows: Arizona: 1.6 mi. S. Superior, Pinal Co. (N=46), Tucson, Pima Co. (N=19); Sonora: 3.3 mi. S. Moctezuma (N=19), 1.6 mi. W. Huasabas (N=20); Baja California Norte: 8.0 mi. N., 1.3 mi. W. San Felipe (N=6).

Results and Discussion

Mitotic C-Band Studies

The Basic Karyotype. In the earlier paper (Patton, 1972) the basic karyotype devoid of supernumerary elements was described as consisting of a diploid number of 46 with 5 pairs of large and 1 pair of small meta-submetacentrics, 4 pairs of medium subtelocentrics, and 12 pairs of medium to small acrocentrics. The X-chromosomes was described as a medium-large submetacentric and the Y a small submetacentric. More recent information substantiates this description with one exception – the morphology of the Y. C-banding unambiguously defines the Y as a medium acrocentric, one of the largest uniarmed elements, and not submetacentric in all populations examined (Figs. 1–4).

In the normal complement, constitutive heterochromatin in the form of C-bands is restricted to the centromeric regions. These centromeric blocks are dense, enlarged, and very conspicuous in all chromosomes of the complement. Except for the Y, no whole arms of heterochromatin are apparent, even among the subtelocentric set. The Y-chromosome heterochromatin is different in staining quality from autosomal C-bands and is perhaps distinct in DNA characterization as well.

This general pattern to the normal complement is rather simple and only two minor deviations were apparent among the individuals examined. In two of the six individuals from Baja California, the smallest pair of acrocentric autosomes displayed distinctive telomeric C-band positive bulbs (Fig. 1a). Additionally, in 2 of the 19 individuals examined from Moctezuma, Sonora, the largest biarmed autosomal pair was polymorphic for a large block of heterochromatin adjacent to and contiguous with the centromeric region in the long arm
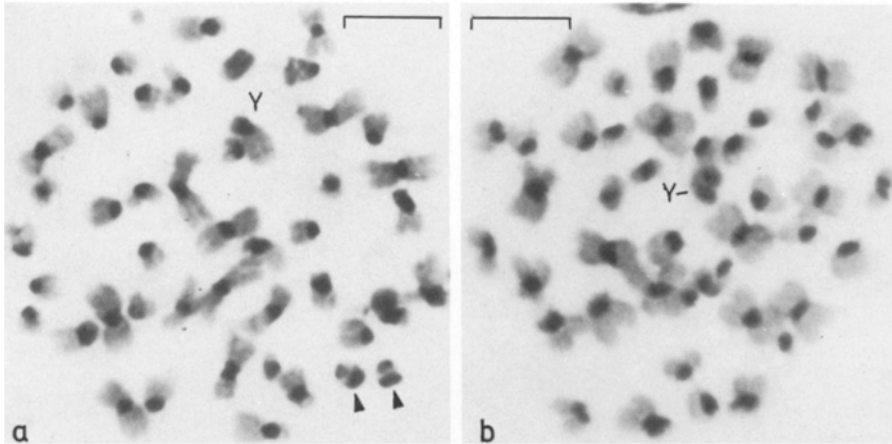
Fig. 1a and b.[1] Distribution of constitutive heterochromatin (C-bands) in *Perognathus baileyi*, 2n = 46 individuals without B-chromosomes (bone marrow preparations). **a** Male specimen from San Felipe, Baja California Norte, Mexico (MVZ 147998). Note acrocentric and heterochromatic Y-chromosome and pair of small acrocentric autosomes with both C-band positive centromeric and telomeric areas (arrows). **b** Male specimen from Tucson, Pima Co., Arizona (MVZ 148321). Note acrocentric and heterochromatic Y

(Fig. 2a). The significance of these variations is not known, but such does suggest that *P. baileyi* is labile in heterochromatin characteristics even in the normal A-chromosome set.

The B-Chromosomes. Patton (1972) distinguished two morphological classes of B-chromosomes in *P. baileyi* based largely on size differences. Type I Bs were small biarmed to uniarmed elements found in nearly all populations with up to 10 per individual. Type II Bs were, on the other hand, rather large and distinctly metacentric chromosomes which were found only in a few populations at the northern and southern margins of the species range. Constitutive heterochromatin patterns, however, indicate that this distinction is somewhat more complex as two Type II Bs are recognizable.

Type I B-chromosomes are totally heterochromatic regardless of their absolute size or centromere position, both of which apparently vary to a slight degree (Fig. 2). The smallest manifestations of this type appear as heterochromatic dots (Fig. 2a and b), whereas the slightly larger, obviously biarmed elements consistently appear with a small pericentromeric region devoid of stain (Fig. 2a, c, and d). The Type I B-chromosomes are readily distinguishable from the single pair of small biarmed autosomes of the A-chromosome set which possess only centromeric heterochromatin (see Figs. 1 and 2).

The two forms of the Type II B-chromosomes are both large biarmed elements of approximate equal size. One of these (here designated IIs, for Sonora) is totally heterochromatic (Fig. 3) while the other (IIa, for Arizona) has large, terminal blocks of apparent euchromatin (C-band negative) on both arms
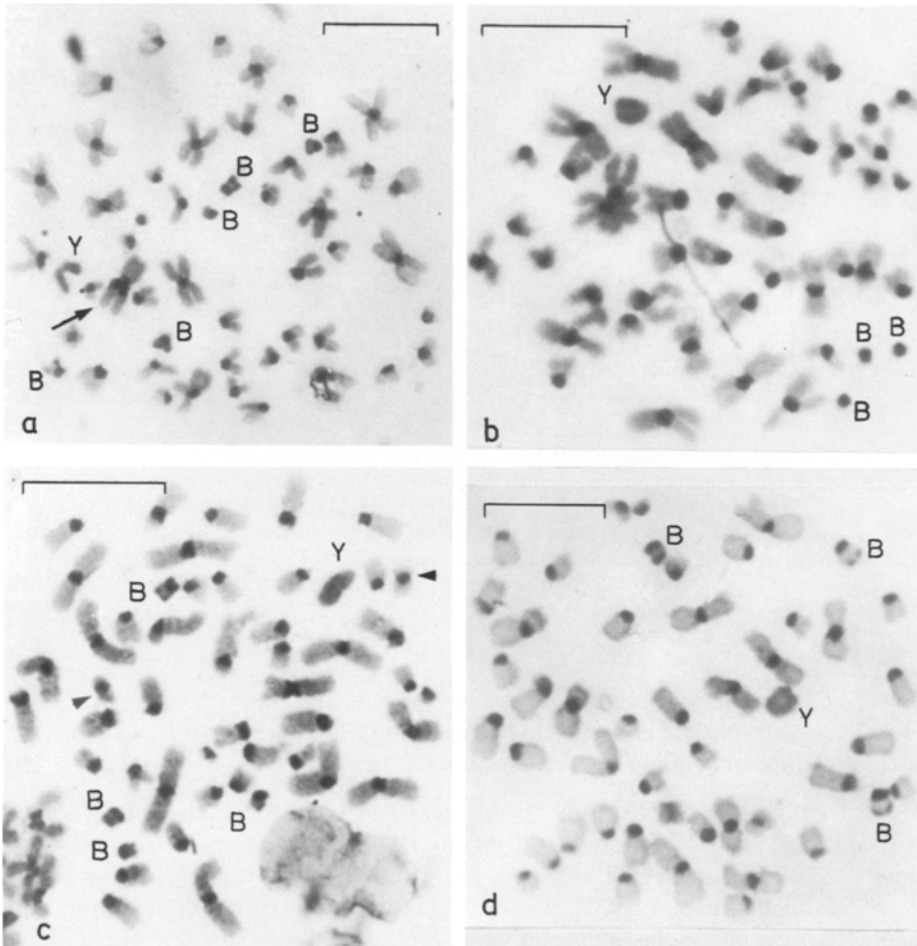
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[1]   Bar in all figures equals 10 μm

Fig. 2a–d. Constitutive heterochromatin (C-band) distribution pattern in *Perognathus baileyi* carrying Type I B-chromosomes (bone marrow preparations). **a** Male specimen from Moctezuma, Sonora, Mexico (MVZ 148939) with 2n = 51 and 5 Type I B-chromosomes. Note enlarged C-band positive region on only one homolog of the largest pair of uniarmed autosomes (arrow). **b** Male specimen from Superior, Pinal Co., Arizona (MVZ 148377) with 2n = 49 and 3 Type I B-chromosomes. **c** Male specimen from Moctezuma, Sonora, Mexico (MVZ 148946) with 2n = 50 and 4 Type I B-chromosomes. Note the biarmed nature of these chromosomes and the difference in C-band pattern between the B-chromosomes and the equivalent sized autosomal biarmed pair (arrows). **d** Male specimen from Huasabas, Sonora, Mexico (MVZ 148921) with 2n = 49 and 3 Type I B-chromosomes

(Fig. 4). These two types of large B-chromosomes have not been found together in the same individual, nor have they been found in different individuals from the same population sample. From current information, Type IIs B-chromosomes occur in low numbers (two or fewer per individual) only in Sonoran populations of *P. baileyi* whereas Type IIa supernumeraries are much more
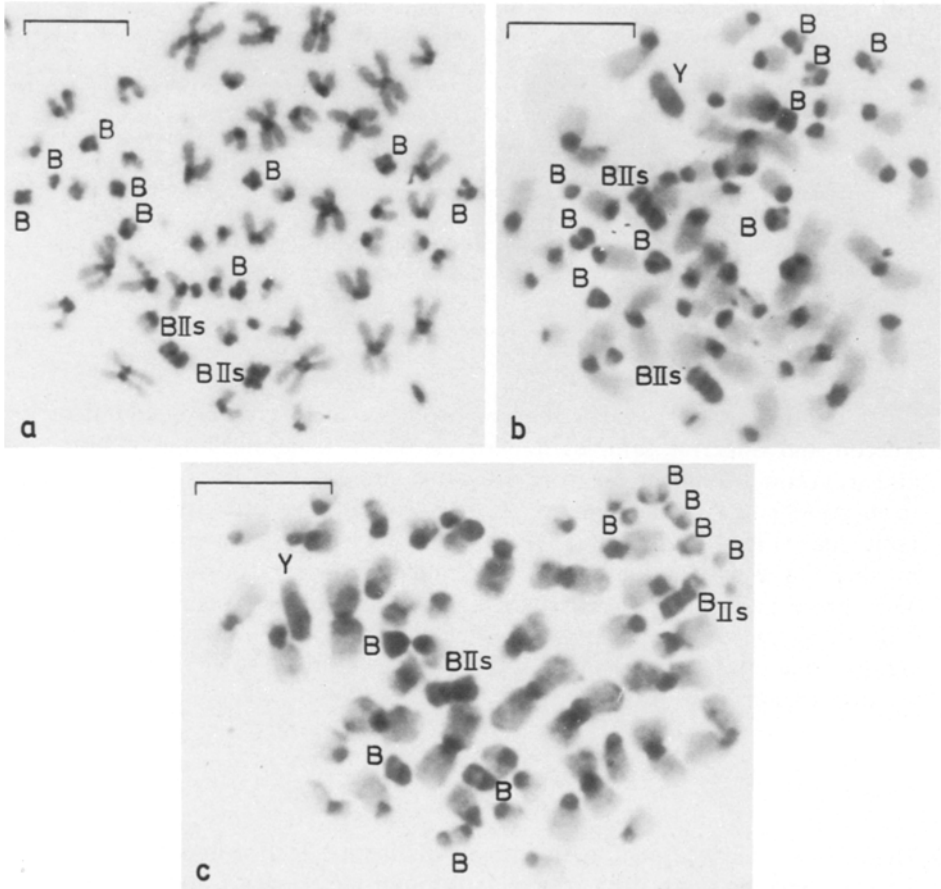
Fig. 3a–c. Constitutive heterochromatin pattern in both Type I and Type IIs B-chromosomes from a male *Perognathus baileyi* from Moctezuma, Sonora, Mexico (MVZ 148943); 2n = 57, including 9 Type I and 2 Type IIs B-chromosomes (bone marrow preparations). Note in particular the size difference between the B-chromosome classes and the apparent compound nature of C-band distribution in the Type IIs B-chromosomes

prevalent (numbering up to seven per individual) but occur only in Arizona populations (see Table 1).

The C-band character of the Type IIs B-chromosomes is one of uniformity. These elements are about twice the size of the largest Type I Bs (Fig. 3a–c), the centromere always has a almost exactly median position, the entire chromosome is heterochromatic, and each arm displays a narrow, weakly staining band about midway along its length. Indeed, the two arms of the Type IIs B-chromosome appear as mirrow images of one another. Never more than two of these elements have been found in any single individual although the range in Type I number in the same individual may be from 2 to 9 (see Table 1 and Patton, 1972:249).

Table 1. Distribution of B-chromosome types in 4 samples of *Perognathus baileyi* for which C-band data are available. The frequency of each type recorded per population is given followed by the numerical range in parentheses

Sample	N	Frequency of individuals with no Bs	Frequency of individuals with		
			Type I	Type IIs	Type IIa
Superior	46	0.16	0.49 (0–3)	0	0.67 (0–7)
Tucson	19	0.32	0.42 (0–2)	0	0.63 (0–3)
Moctezuma	19	0	1.00 (3–9)	0.16 (0–2)	0
Huasabas	20	0	1.00 (1–6)	0.05 (0–1)	0

In contrast, the Type IIa B-chromosomes which have been found in the Tucson and Superior samples in Arizona show some variation in both size and arm ratio. Moreover, far from being uncommon, these Bs are the ubiquitous form present in Arizona samples as up to seven have been found in a single individual (Fig. 4a and Table 1). Type IIa B-chromosomes are characterized by their large size and apparent euchromatic terminal portions (Fig. 4a–d). They are usually uniform in length and amount of heterochromatin content (Fig. 4a–c), but often appear as divergent in size. Such differences apparently are due to additions or deletions in the C-band positive rather than the C-band negative regions (Fig. 4d).

Meiosis

Meiosis was analyzed in 17 male individuals from Superior and 16 males from Tucson, Arizona, with both prophase through metaphase I and metaphase II figures examined. Meiosis in the normal complement of *P. baileyi* is as expected: 23 bivalents at the first meiotic division and 23 univalents at the second. The five pairs of large biarmed autosomes generally show chiasmata on both arms with all other autosomes exhibiting only a single chiasma in diplotene. The X and the Y pair end-to-end, with the Y synapsing with the long arm of the X. It is not possible to tell if this association is chiasmate. C-band studies of meiosis I (Fig. 5a and b) indicate that pairing among the acrocentric autosomes is almost invariably between the telomeres of the long arms, not at the centromeric regions. The X and the Y undergo a prereductional segregation.

B-chromosomes, either Type I or Type IIa, are usually found as univalents at meiosis I (Fig. 6a and b) although multivalents are often seen (Fig. 6c and d). Multivalent associations observed include bivalents, trivalents, and even an occassional tetravalent in one individual male with 5 Type IIa B-chromosomes. In no cases were B-chromosomes observed to pair with a member of the A-chromosome set. These data indicate that, while the B-chromosomes are unique relative to the normal complement, there is considerable homology between them. The similarity in size, morphology, and C-banding pattern within each of the B-chromosome classes provides additional evidence for homology
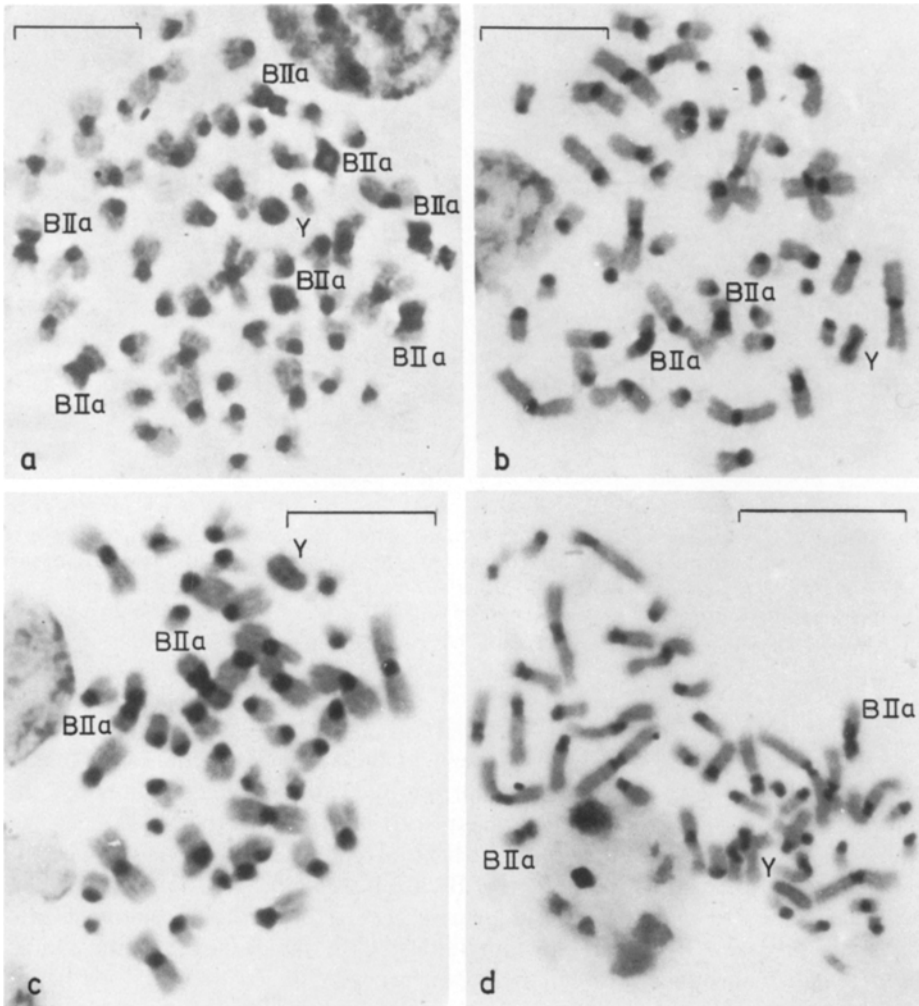
Fig. 4a–d. Constitutive heterochromatin (C-band) characteristics of Type IIa B-chromosomes from Arizona individuals of *Perognathus baileyi*. Note C-band positive pericentromeric region and C-band negative terminal portions on each arm of the B-chromosome. **a** Male individual from Superior, Pinal Co. (MVZ 148365); 2n=53 with 7 Type IIa B-chromosomes (bone marrow preparation). **b** Male individual from Tucson, Pima Co. (MVZ 148319); 2n=48 with 2 Type IIa B-chromosomes (bone marrow preparation). **c** Male individual from Tucson, Pima Co. (MVZ 148322); 2n=48 with 2 Type IIa B-chromosomes (bone marrow preparation). **d** Male specimen from Superior, Pinal Co. (MVZ 148379); 2n=48 with 2 Type IIa B-chromosomes (spermatogonial metaphase). Note disparate size relationship of the two B-chromosomes

between Bs within each categorical type. It should be stressed, however, that almost all observations on meiotic behavior pertain only to the Type IIa B-chromosomes which have the apparent euchromatic, or at least C-band negative, terminal portions on each arm.

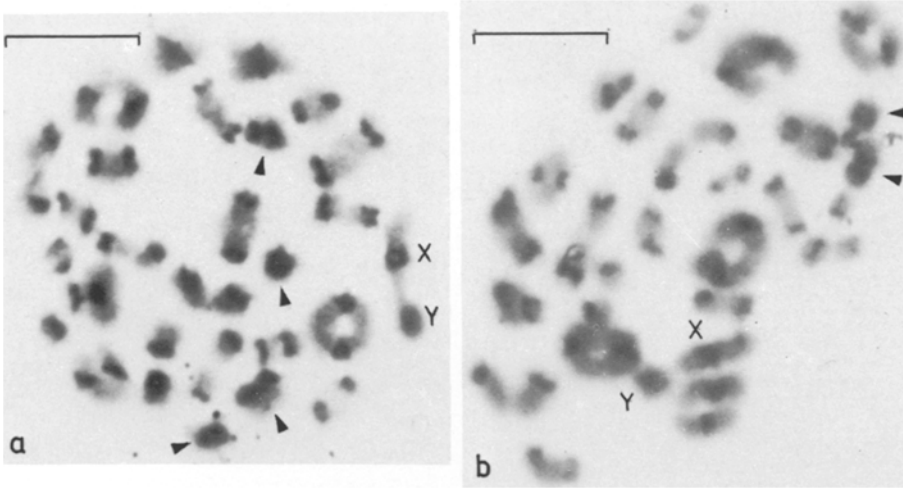Segregation of Type IIa B-chromosomes into secondary spermatocytes is

Fig. 5a and b. Constitutive heterochromatin (C-band) pattern of selected first metaphase cells of *Perognathus baileyi* from Superior, Pinal Co., Arizona (testicular preparations). **a** Male specimen (MVZ 148369) with n=27, including 23 bivalents of the A-chromosome set and 4 univalent Type IIa B-chromosomes (arrows). **b** Male specimen (MVZ 148379) with n=25, including 23 univalents of the A-chromosome set and 2 univalent Type IIa B-chromosomes (arrows)

not random as the number of Bs present in metaphase II figures was higher than expected. These data are summarized in Table 2 which compares the haploid number observed in metaphase I to that in metaphase II cells for individuals with a given number of B-chromosomes. This comparison permits the determination of the randomness of B-chromosome distribution into secondary spermatocytes and hence a judgement as to their final assortment into the male gametes. For example, individuals with one B-chromosome would be expected to produce 50% of their gametes with no Bs and 50% with one B. The observed B distribution for such individuals of *P. baileyi* is, however, at considerable odds with this expectation (Table 2). Indeed, individuals with one B-chromosome have 70%, rather than 50%, of their secondary spermatocytes with a single B.

Table 2 provides data on the assortment of Type IIa B-chromosomes in individuals with from one to five such elements. A significant deviation from randomness was found in individuals with 1, 2, or 4 B-chromosomes while those with 3 or 5 B-chromosomes showed a similar, but marginally non-significant deviation. In all cases, deviations were toward a higher number of Bs per secondary spermatocyte than expected. These data suggest that the average sperm produced by a given individual male will have the same or a higher number of B-chromosomes than that particular individual.

Whether females likewise exhibit a skewed assortment of B-chromosomes is not known. However, unless females preferentially lose B-chromosomes in egg formation, and hence offset the increase in B number per sperm, an observed
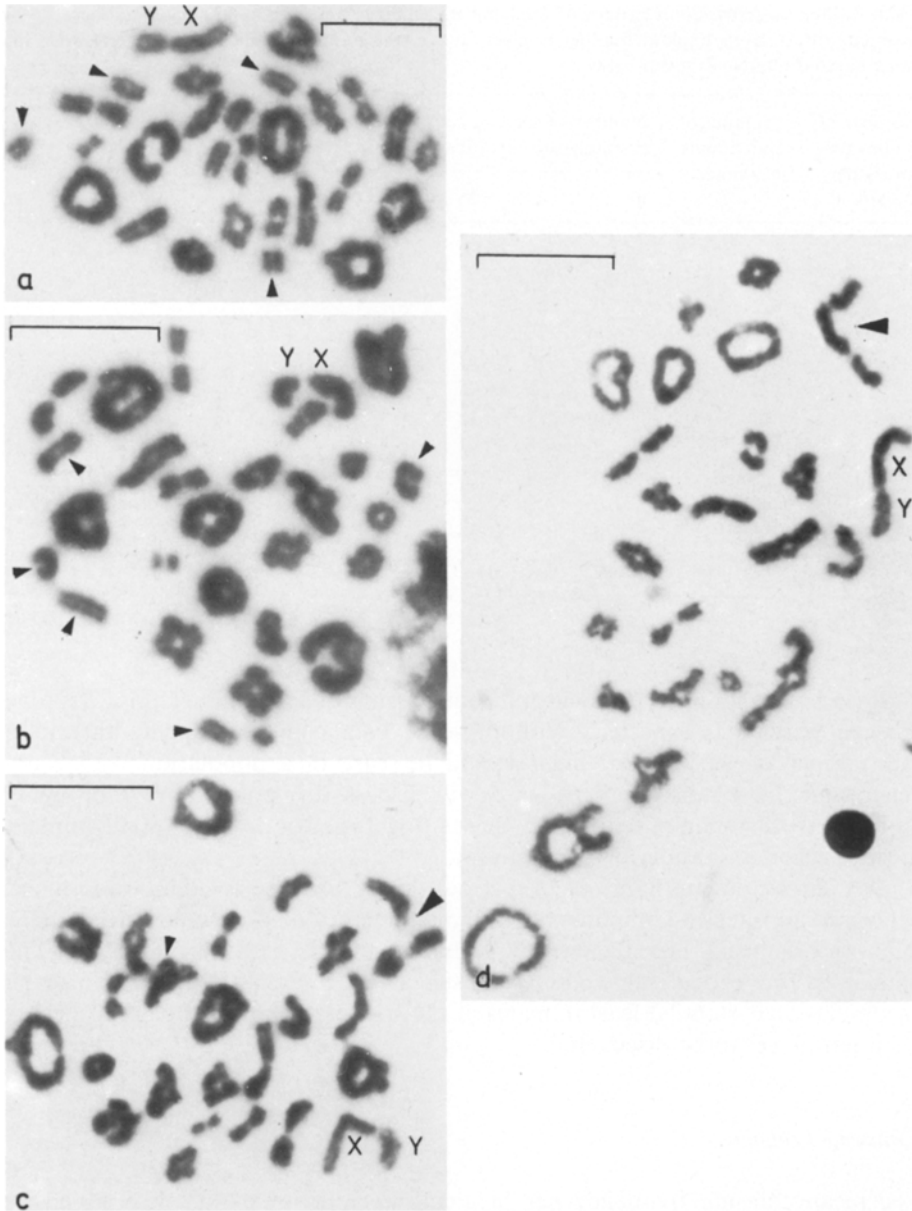
Fig. 6a–d. Selected first meiotic division cells of *Perognathus baileyi* from Superior, Pinal Co., Arizona. **a** Male specimen (MVZ 148369) with 2n=27, including 4 univalent Type IIa B-chromosomes (arrows). **b** Male specimen (MVZ 148372) with n=28, including 5 univalent Type IIa B-chromosomes (arrows). **c** Same individual as in Fig. 6a but with n=25, including 1 univalent (small arrow) and 1 trivalent Type IIa B-chromosome association (large arrow). **d** Male specimen (MVZ 148370) with n=24, including a single trivalent Type IIa B-chromosome association (arrow)

Table 2. Meiotic distribution pattern of Type IIa B-chromosomes. The number of metaphase I cells counted with a given haploid number is given above, the number of metaphase II cells with the same haploid number is given below

Number of B-chromosomes per individual	Number of individuals examined	Number of meiotic cells examined (metaphase I/metaphase II)						Deviation from random assortment
		n = 23	24	25	26	27	28	
0	5	$\frac{36}{28}$						—
1	6	$\frac{0}{8}$	$\frac{43}{19}$					$\chi^2 = 4.481, p < 0.01$
2	6	$\frac{0}{6}$	$\frac{20}{6}$	$\frac{21}{15}$				$\chi^2 = 13.001, p < 0.001$
3	10	$\frac{0}{8}$	$\frac{13}{7}$	$\frac{14}{16}$	$\frac{31}{13}$			$\chi^2 = 4.963$, ns
4	3	$\frac{0}{0}$	$\frac{4}{7}$	$\frac{5}{7}$	$\frac{12}{12}$	$\frac{9}{6}$		$\chi^2 = 11.741, p < 0.05$
5	3	$\frac{0}{0}$	$\frac{0}{0}$	$\frac{3}{2}$	$\frac{6}{6}$	$\frac{15}{4}$	$\frac{6}{4}$	$\chi^2 = 10.097$, ns

increase in the number of B-chromosomes per individual in offspring relative to their parents is expected. Without some balancing mechanism, therefore, the number of Bs per individual would increase in a population with every generation. In a subsequent paper, I will discuss this point more thoroughly and describe a system of temporally fluctuating Type IIa B-chromosome number in the Tucson and Superior populations.

Accumulation mechanisms of various kinds are nearly ubiquitous in an hence are an integral component of the maintenance of B-chromosome systems in most organisms (see reviews by Müntzing, 1974, and Hewitt, 1973). The data given above for *Perognathus baileyi* suggest the presence of a B-chromosome accumulation system, at least in males of the species, although the exact mechanism has as yet to be discovered.

Chiasma Frequency

The mean chiasma frequency per bivalent per individual was determined by direct count of 10 to 20 diplotene-diakinetic figures. The data available for the 33 males examined are given in Table 3. As described above, typically each of the 5 large biarmed autosome pairs exhibit one chiasma on each arm while each uniarmed pair associates with a single chiasma. Thus, the mean chiasma frequency for individuals with no B-chromosomes in their complements is 1.234 (Table 3). However, individuals with one or more Type IIa B-chromosomes as a group do show a slightly significant increase in chiasma frequency within the A-chromosome set (mean = 1.251 per bivalent, $p < 0.05$; Table 3),

Table 3. Summary of chiasma frequency statistics per bivalent for the A-chromosome set in individuals with from zero to 5 Type IIa B-chromosomes. Data from the Tucson and Superior samples

Statistics	Number of B-chromosomes					
	0	1	2	3	4	5
Number of specimens examined	5	6	6	10	3	3
Number of metaphase I cells examined	36	43	41	58	30	30
$\overline{X}$ chiasmata per bivalent	1.2341	1.2565	1.2635	1.2480	1.2500	1.2393
Standard error	0.004	0.014	0.007	0.008	0.008	0.005
Grand mean $\pm$ SE	1.2514 $\pm$ 0.009					
Significance level	$\chi^2 = 3.076, p < 0.05$					

an increase that is manifested by both more than two chiasmata formed within the large biarmed autosomes as well as a double chiasmate relationship within the subtelocentric or acrocentric group autosomes. The relationship between number of Bs and chiasma frequency is not an addative one, however, as the latter is highest in individuals with 2 B-chromosomes relative to those with fewer or greater numbers. Individuals with 5 B-chromosomes have a mean chiasma frequency nearly at the level recorded for individuals without Bs (Table 3). Hence, chiasma frequency is related not only to presence of Bs but apparently it is optimized at a particular frequency of B-chromosomes per individual. Whether this observation will hold upon examination of other populations with both different numbers and/or types of B-chromosomes remains to be seen.

An increase in recombination at the chiasma level resulting from B-chromosome presence has been a rather common observation in grasshopper and other cytogenetic systems (see John, 1973, for review). Hence, supernumeraries are thought to owe their adaptive value, at least in part, to their ability to produce increased variability through the development of novel recombinant genotypes. It is questionable, however, whether the increase in chiasma frequency observed here for *P. baileyi* should be judged in this light. On the surface, the maximal increase in chiasma frequency per complement (mean of 28.38 for individuals with no B-chromosomes to 29.06 for those with 2 B-chromosomes), while statistically significant, appears insufficient to be of biological significance.

Origin of B-Chromosomes

A major question surrounding all known supernumerary systems concerns their origin. While a complete understanding of the origin of the B-chromosome types of *P. baileyi* is some distance away, there are several aspects of the current data base from which reasonable hypotheses can be developed.

Mechanisms which have been implicated in the origin of B-chromosomes

include: polysomy of small autosomes, autosomal or X-chromosomal deletion products, isochromosome formation of X-chromosomes, and remnant centromeres following fusion events. Hewitt (1973) has reviewed most of these mechanisms with regard to orthopteran B-chromosome systems. For *P. baileyi,* since there are three definable types of B-chromosomes, there is thus the possibility of separate mechanisms for the origin of each.

In the earlier paper (Patton, 1972), I concluded that the Type I B-chromosome originated as a centromeric product from the fusion events presumed to have occurred in the formation of the 5 large autosomal biarmed pairs. This suggestion is still the most viable explanation for this class of B-chromosomes in *P. baileyi.* The enlarged C-band positive centromeric regions of all autosomal chromosomes and a similar C-band positive nature of Type I Bs support this contention. The second most appealing explanation of origin is via polysomy of any of the small acrocentric or biarmed elements of the A-chromosome set followed by heterochromatization. While I am in less favor of this possibility due to the known deleterious effects which often accompany polysomy, a final decision between these two mechanisms must await characterization of the DNA in Type I B-chromosomes versus centromeres, and so forth.

Type IIs B-chromosomes appear most likely to be derived directly from Type I Bs. The totally heterochromatic nature with internal segmentation of C-bands into interstitial blocks of equal size on each arm suggests an origin either by tandem duplication of a single Type I B or by tandem fusion of 2 or more Type I B-chromosomes. The fact that these elements are only found in populations with high numbers of Type I B-chromosomes is further support for this idea (see Table 1 and Patton, 1972).

The origin of Type IIa B-chromosomes poses somewhat of an enigma. The similarity to Type IIs Bs in gross appearance suggests a link between them, but this possibility loses force in comparisons of their C-band patterns. Type IIa supernumeraries are considerably more variable in size than other types known for *P. baileyi* (see Fig. 4d, for example) with the difference largely resting in the amount of C-band positive chromatin present. This suggests that the smaller version of this type is perhaps the original version. Hence a logical interpretation of origin is via either polysomy or as a deletion product of an A-chromosome set member with subsequent duplications within the C-band positive areas to promote larger size. The fact that C-band negative chromatin continues to comprise a significant portion of the Type IIa B-chromosome is difficult to understand if, indeed, this material is genetically active euchromatin. However, since the replication pattern of any of the B-chromosomes of *P. baileyi* is unknown, the possibility remains that the entire Type IIa B-chromosome is late replicating despite containing both C-band positive and negative chromatin.

Conclusion

Three classes of supernumeraries are recognizable based on gross morphology and heterochromatin content: (1) Type I Bs are small uniarmed to biarmed chromosomes, totally C-band positive; (2) Type IIs Bs are moderately large

biarmed chromosomes, totally heterochromatic with a segmental appearance of C-band blocks on each arm; and (3) Type IIa Bs, which are likewise large biarmed elements, but have large C-band negative terminal blocks on each arm.

Meiotic data, available only for the Type IIa B-chromosomes, show that these elements are found as univalents or in various multivalent combinations in the first meiotic division. Assortment of these chromosomes from meiosis I to meiosis II is decidedly non-random, suggesting the presence of an accumulation mechanism in males. Chiasma frequency in the A-chromosome set is seen to increase slightly in comparisons of individuals with to those without B-chromosomes. Individuals with different numbers of Bs do show a differential level of chiasma increase with a peak reached in individuals with two Type IIa B-chromosomes. It is argued, however, that while the overall increase is statistically significant it may not be biologically important.

Finally, the three classes of B-chromosomes are considered to have different origins although that of the Type IIs class is tightly dependent on Type I Bs. Type I B-chromosomes are likely to be centromeric remnants from prior fusion events with Type IIs Bs being derived from this group either by tandem duplication or tandem fusions. Type IIa Bs are thought to have a totally separate origin and most likely represent partially heterochromatized polysomics or deletion products of the A-chromosome set.

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