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Two chromosomal forms of white-footed mice (Peromyscus leucopus) exist in Kansas, Oklahoma, and northern Texas. These differ by three pericentric inversions on chromosomes 5, 11, and 20. Individuals representative of the northeastern cytotype and the southwestern cytotype were collected from Kansas populations not in contact with each other, and hybrids between the two cytotypes were collected from within the zone of contact in Oklahoma. Breeding pairs were established, and hybrids, whether collected in the zone of contact or produced in the lab, showed no reduction in fertility. Chromosomes of hybrid individuals collected from within the zone of contact in Oklahoma were compared to chromosomes of hybrids formed between mice collected outside the zone of contact. Silver-stained spermatocyte spreads prepared from hybrids produced within the zone of contact and from hybrids produced from populations not formerly in contact were observed during meiosis. These spreads showed heterosynaptic pairing of the inverted regions of the hybrid's chromosomes. No inversion loops were observed. Heterosynaptic pairing, which is interpreted as a mechanism

to avoid hybrid infertility, was not found to be the result of an adaptive mechanism that is unique to individuals within the zone of contact, but one which is inherent within the species itself.

PERICENTRIC INVERSIONS AS A REPRODUCTIVE ISOLATING MECHANISM IN WHITE-FOOTED MICE (*PEROMYSCUS LEUCOPUS*)

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It is said that when you see a turtle sitting on a fence post, you know he had some help. I would like to express here my sincere appreciation to all those who assisted me with this project.

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FOREWORD

This thesis is presented in the form of a paper prepared in a style appropriate for Cytogenetics and Cell Genetics to which it will be submitted for publication.

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PERICENTRIC INVERSIONS AS A REPRODUCTIVE ISOLATING MECHANISM IN DEER MICE (PEROMYSCUS LEUCOPUS)

Introduction

Two chromosomal forms of white-footed mice (Peromyscus leucopus) exist in Kansas, Oklahoma, and northern Texas. These chromosomal forms differ by three pericentric inversions on chromosomes 5, 11, and 20 (Baker et al., 1983). In the animals designated as having the northeast cytotype, chromosomes 5 and 11 are acrocentric and chromosome 20 is metacentric, while the southwest cytotype has an acrocentric chromosome 20, and metacentric chromosomes 5 and 11. In Oklahoma the two cytotypes meet in a broad zone of contact that contains F_1 hybrids and backcross hybrids of the two parental cytotypes (Stangl, 1986). Both cytotypes occur in Kansas, yet, while there does not seem to be any habitat discontinuity to separate them, no zone of contact between the two cytotypes has been identified within Kansas.

One of the important concepts in evolutionary biology is that of reproductive isolating mechanisms. These mechanisms allow species to occupy the same area and yet maintain separate gene pools by employing characteristics or traits that serve to prevent or greatly reduce the production of fertile hybrids between the species (Dobzhansky, 1970). Initially, genetic isolating mechanisms arise primarily by chance (Mayr, 1963) as the gene pools of

two allopatric populations diverge from each other sufficiently to prevent the production of fertile hybrids (Ehrman, 1962). These genetic barriers represent post-mating isolating mechanisms. Upon contact of two previously isolated populations, natural selection will act in one of two ways. The genetic post-mating isolating mechanisms between the hybrids may be reinforced by selection acting to establish a pre-mating isolating mechanism such as behavioral differences that would prevent mating (Ehrman, 1965; Waage, 1979). Alternatively, selection may act to reduce the infertility of the hybrids, in which case the two populations will tend to fuse into one species (Stebbins and Daly, 1961).

Pericentric inversions have traditionally been thought to act as reproductive isolating mechanisms within a species. Since McClintock's (1931,1933) initial observations of chromosome pairing at meiosis in inversion heterozygotes of Zea mays, such heterozygosity has been commonly assumed to result in significant reduction in fertility. White (1978) reported that the presence of one inversion could reduce the fertility by up to 50% in a hybrid individual. Three inversions could reduce fertility of a hybrid between the parental cytotypes by 88%. However, in the broad zone of contact that exists between the two

parental cytotypes of Peromyscus in Oklahoma, there is no evidence of hybrid sterility (Stangl, 1986).

Greenbaum and Reed (1984) examined populations of a closely related species (Peromyscus maniculatus) in which two cytotypes, differing by an inversion, exhibit a zone of contact. They found evidence of heterosynaptic pairing of the inverted segment in individuals heterozygous for a pericentric inversion. Heterosynapsis was hypothesized to be a mechanism that might eliminate production of the duplication and deletion chromatids expected from crossing-over within pericentric inversion loops. If crossing over does not occur, there would be no reduction in fertility.

The purpose of this study was to compare chromosomes of hybrid individuals collected from within the zone of contact in Oklahoma to chromosomes of hybrids formed between mice collected outside the zone of contact. If natural selection has served to reduce the effects of the inversions in the zone of contact, and hence to reduce infertility, then a reduction in fertility in the hybrids produced by mice not from the zone of contact would be expected. Alternatively, if P. leucopus has the ability to pair heterosynaptically during meiosis, then hybrids from the contact zone and from mice not from the zone should have the same fertility and exhibit the same pairing behavior during meiosis.

Fertility of hybrid individuals was measured both directly, through controlled breeding experiments, and estimated indirectly by examining the pairing behavior of the chromosomes during meiosis. This study used silver staining of the synaptonemal complex (SC) protein to identify the position of respective chromosomes. The staining technique used to observe the SC protein is relatively simple and hybrid testicular material can be observed after maintaining mice in captivity for only one generation rather than for several generations, as is required to directly evaluate the degree of hybrid fertility.

Materials and Methods

Individuals of Peromyscus leucopus that were representative of the northeastern cytotype, the southwestern cytotype, and hybrid individuals were trapped in Kansas and Oklahoma. Collection sites were selected on the basis of previously mapped ranges of the two cytotypes and hybrid zones as reported by Stangl (1986). Animals of the southwest cytotype were captured at Site I, located at Pratt County Lake, Pratt County, Kansas. Animals of the northeastern cytotype were captured at site II, located at Marion Reservoir, Marion County, Kansas. Hybrids were captured within the 20-km wide hybrid zone identified in Seminole and Pottawatomie counties in Oklahoma along Oklahoma State Highway 9. Animals were captured in Sherman live traps that were baited with rolled oats and peanut butter. Captured animals were transported to Emporia State University, where they were ear tagged for identification of individuals and established as breeding pairs.

Animals were maintained at approximately 22^0 C with a light cycle of 18 hours of light and 6 of dark. Water and rodent laboratory chow were provided ad libitum. Two to four animals were placed in each 28.5 x 19 x 12.5 cm cage. Reciprocal crosses were established between P. leucopus of the northeast and the southwest cytotypes. Individuals collected from within the hybrid zone were also arranged in

mating pairs to establish hybrid fertility.

Testicular material for meiotic analysis was prepared for electron microscopy by the surface spreading technique of Counce and Meyer (1973), as modified by Moses (1977b). Meiotic preparations were stained with silver nitrate as described by Howell and Black (1980). These preparations were then mounted on 100-square mesh copper grids and examined using a Hitachi HS-8 transmission electron microscope at 50kV. Zygotene and pachytene nuclei were assigned to substages according to Greenbaum et al. (1986).

Karyotypes were obtained from metaphase spreads from study animals posthumously to confirm the cytotypes. Spreads were prepared using a modification of the bone marrow technique of Lee and Elder (1980). These chromosomal preparations were then G-banded following the procedures of Seabright (1971). G-banded chromosomes were compared to published photographs (Stangl, 1986) to identify individuals as having either a southwest or northeast cytotype or as being hybrid between those cytotypes. A total of four pairs of each of chromosome number 5 and 11 were evaluated for each animal.

Museum specimens of study animals are housed in the Schmidt Museum of Natural History at Emporia State University, Emporia, Kansas.

Results

In the laboratory, breeding pairs of mice caught within the hybrid zone in Oklahoma reproduced normally, and showed no signs of hybrid infertility (Table 1). Mice caught within areas previously established as the northeast and southwest zones produced hybrids when caged together without exhibiting any pre-mating or post-mating isolating mechanisms. The hybrids of these unions also showed no apparent reduction in fertility when mated among themselves, or back to the parental cytotypes.

Ten to fifteen silver-stained spreads from each of 6 animals were observed. One animal was a hybrid collected from within the hybrid zone, three were lab-bred hybrids, and two were parental types. Silver-stained spermatocyte spreads from these six individuals revealed synaptonemal spreads in which no inversion loops were observed. Spreads observed in late zygotene to late pachytene showed complete pairing of all chromosomes. Thus, not only were homologous chromosomes of the parental types completely paired, (Fig. 1, 2), but complete pairing of non-homologous regions of chromosomes from hybrid individuals was also observed (Fig. 3-6). Furthermore, since chromosomes were completely paired even in late zygotene, synaptic adjustment was not observed.

Several chromosomal aberrations were noted in the chromosomes of the animals observed. Figure 7 shows a multivalent observed in early pachytene from an individual from Marion County. This same animal also showed incomplete pairing of another nearby chromosome (Fig 8) that had an unpaired end and a buckle. These configurations were only observed in one spread from this animal. Several other chromosomal aberrations were noted in this individual, which was the oldest at the time of sacrifice.

TABLE 1-- Pairings and reproductive success of *Peromyscus leucopus* collected in Kansas and Oklahoma. Successful mating pairs are defined as pairs which produced litters.

Cytotypes of Pairs	Number of Mating Pairs		
Male X Female	Successful	Unsuccessful	Total
Northeast X Southwest	7	1	8
Southwest X Northeast	6	2	8
Hybrid X Hybrid	9	1	10
Lab-bred Hybrid X Lab-bred Hybrid	3	0	3

Fig. 1. Partial late zygotene silver-stained spread of individual of northeastern cytotype showing the chromosomal pairing of homologous chromosomes. Bar represents 10 μm.

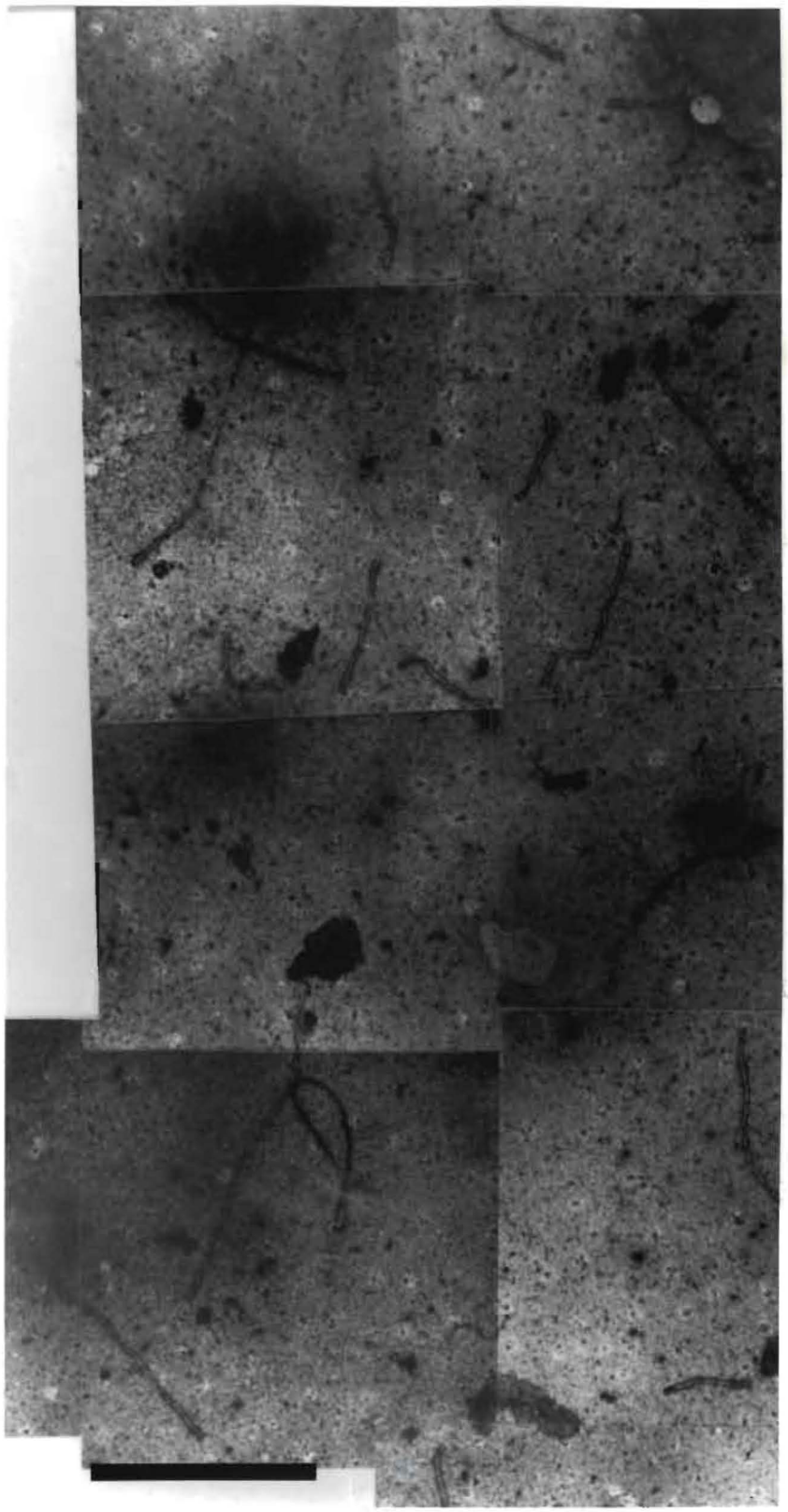


Fig. 2. Mid-pachytene silver-stained spread of individual of northeast cytotype showing the pairing configuration of homologous chromosomes. Bar represents 10 μm.

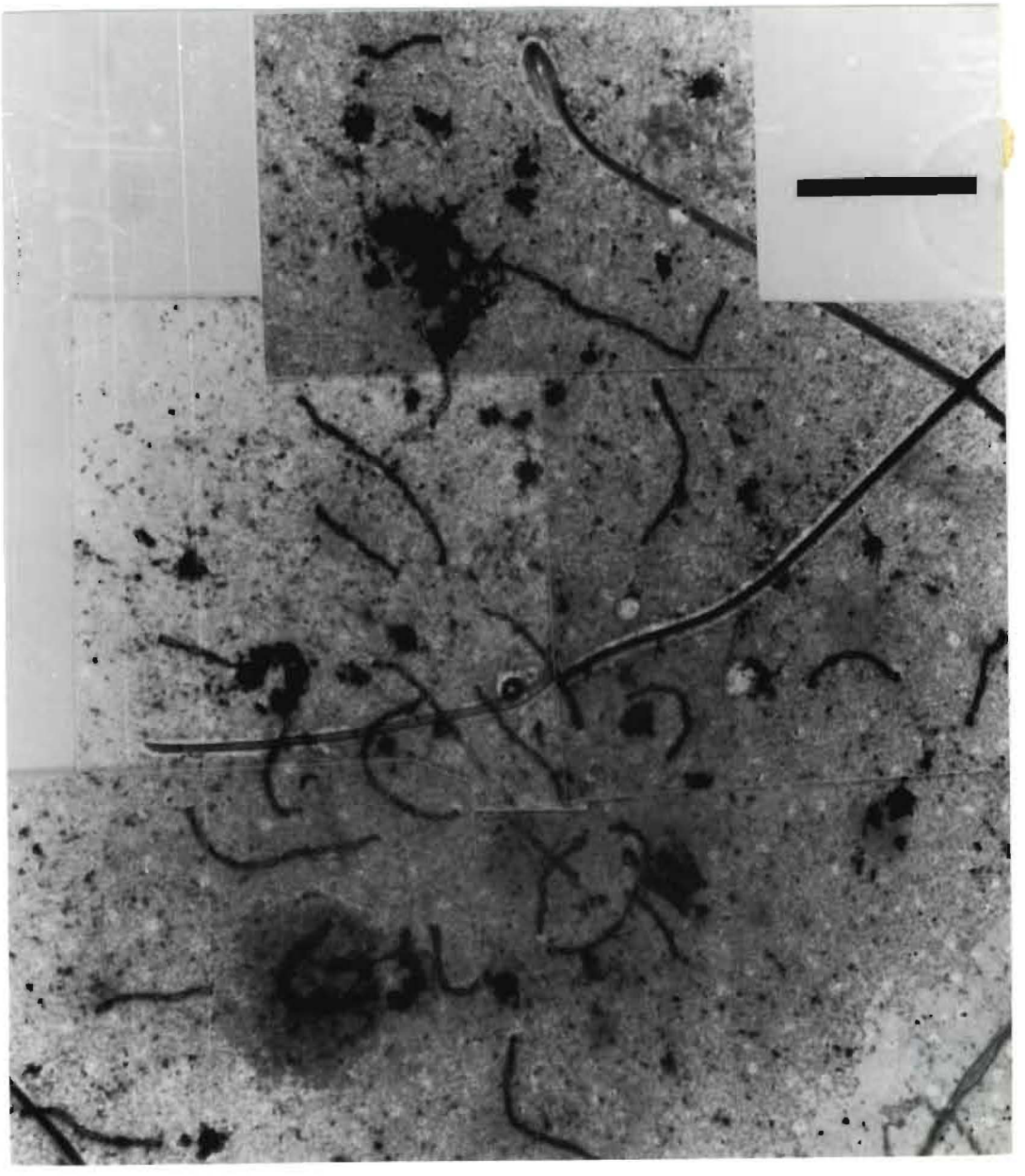


Fig. 3. Late zygotene silver-stained spread of laboratory-bred hybrid showing heterosynapsis of the inverted regions. Bar represents 5 μm.

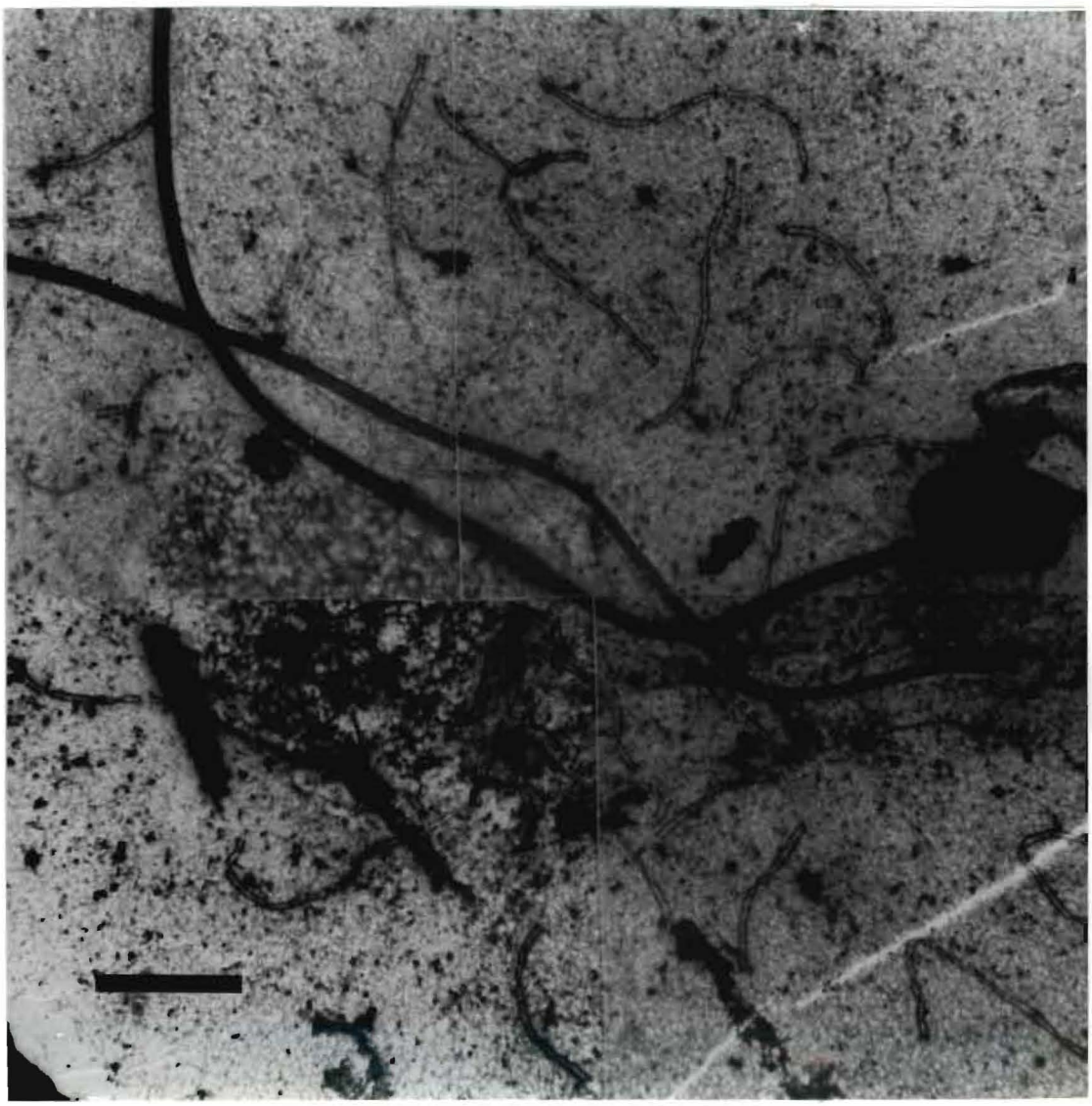


Fig. 4. Late pachytene silver-stained spread of laboratory-bred hybrid showing complete pairing of all chromosomes, and heterosynapsis of inverted regions. Bar represents 5 μm.

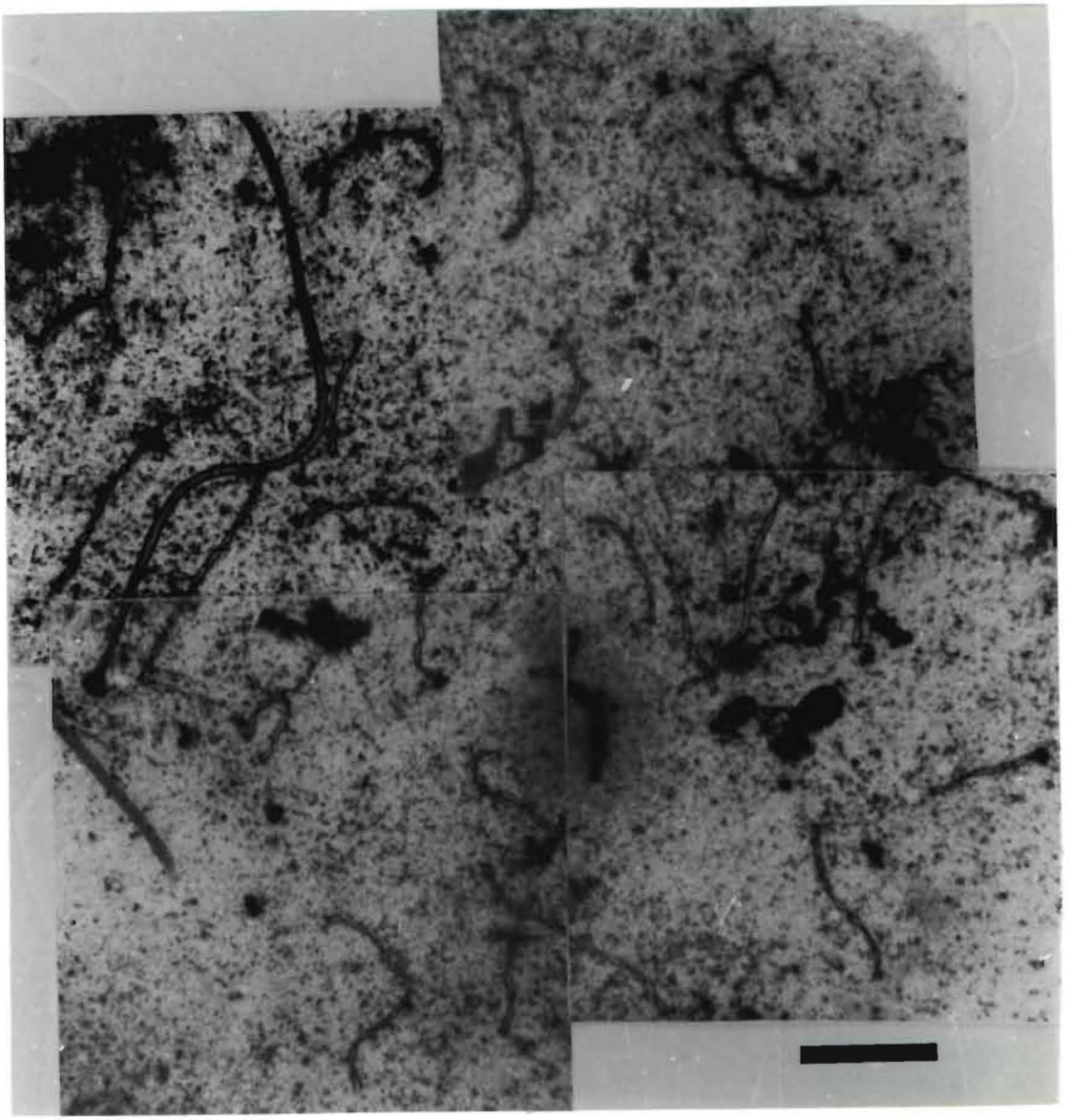


Fig. 5. Late zygotene silver-stained spread of hybrid captured in the hybrid zone showing complete pairing of all chromosomes and heterosynapsis of inverted regions. Bar represents 5 μm.

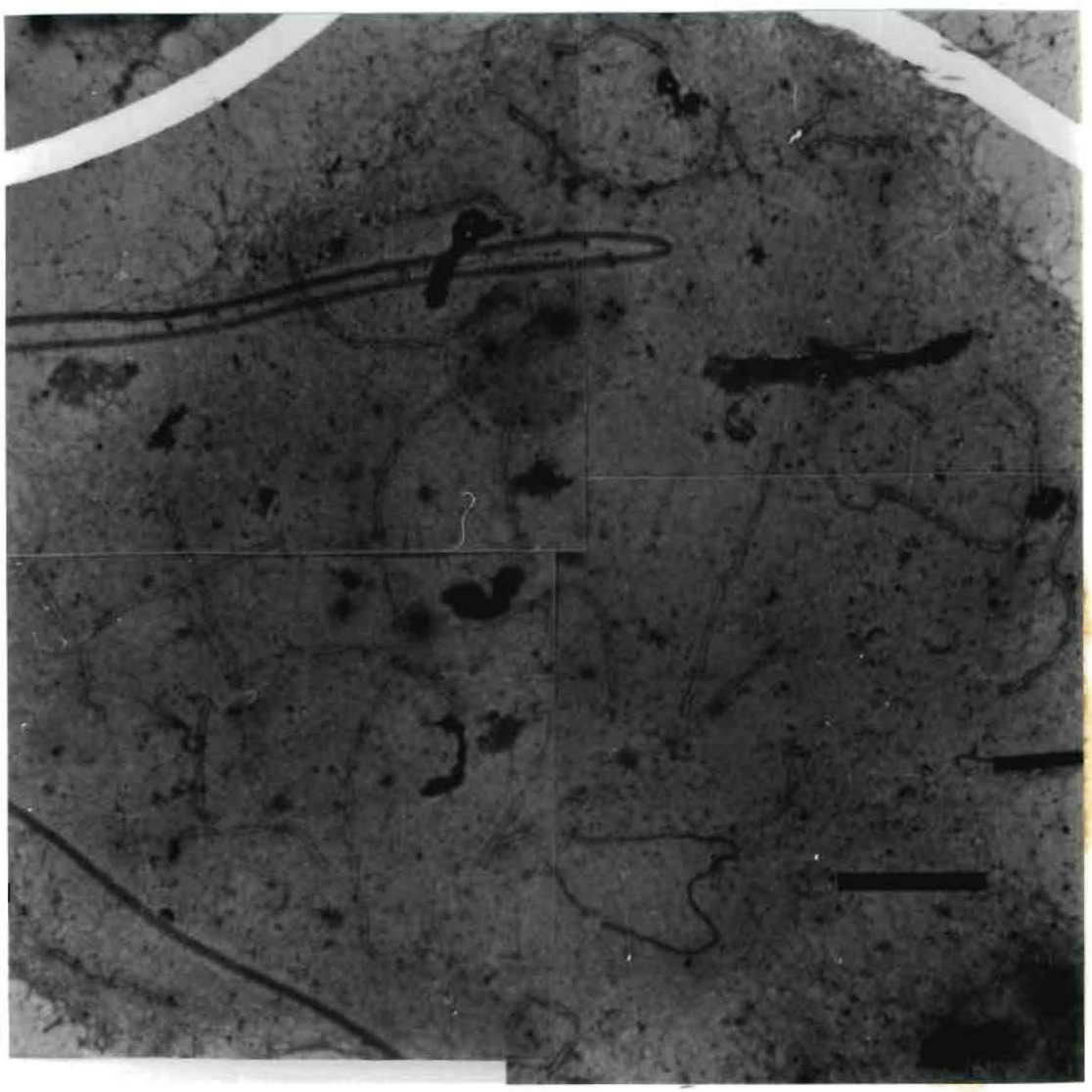


Fig. 6. Mid-pachytene silver-stained spread of hybrid from zone of contact showing complete pairing of all chromosomes. Bar represents 5 μm.

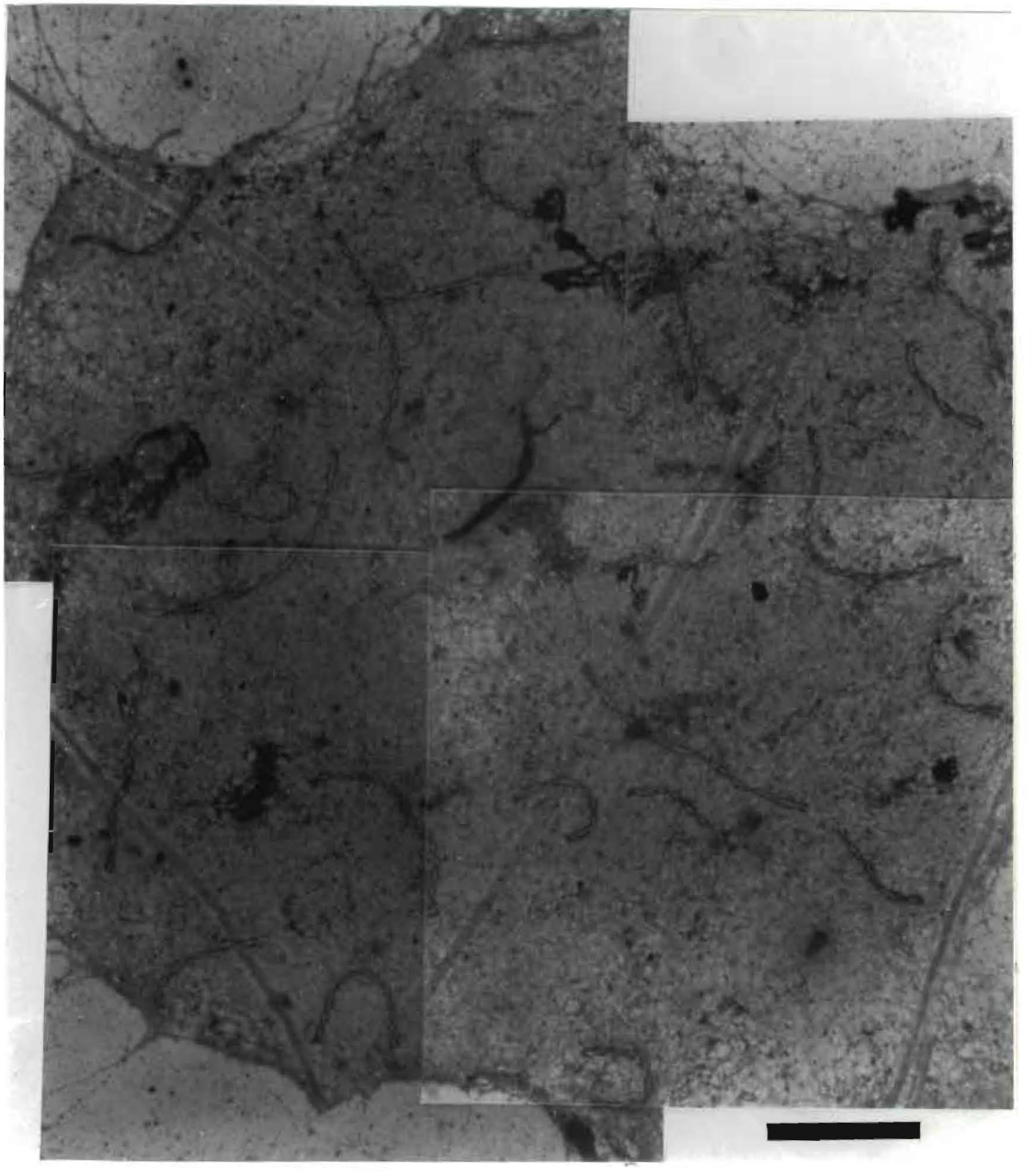


Fig. 7. Early pachytene silver-stained spread of individual of northeast cytotype showing multivalent chromosomes. Bar represents 5 μm.

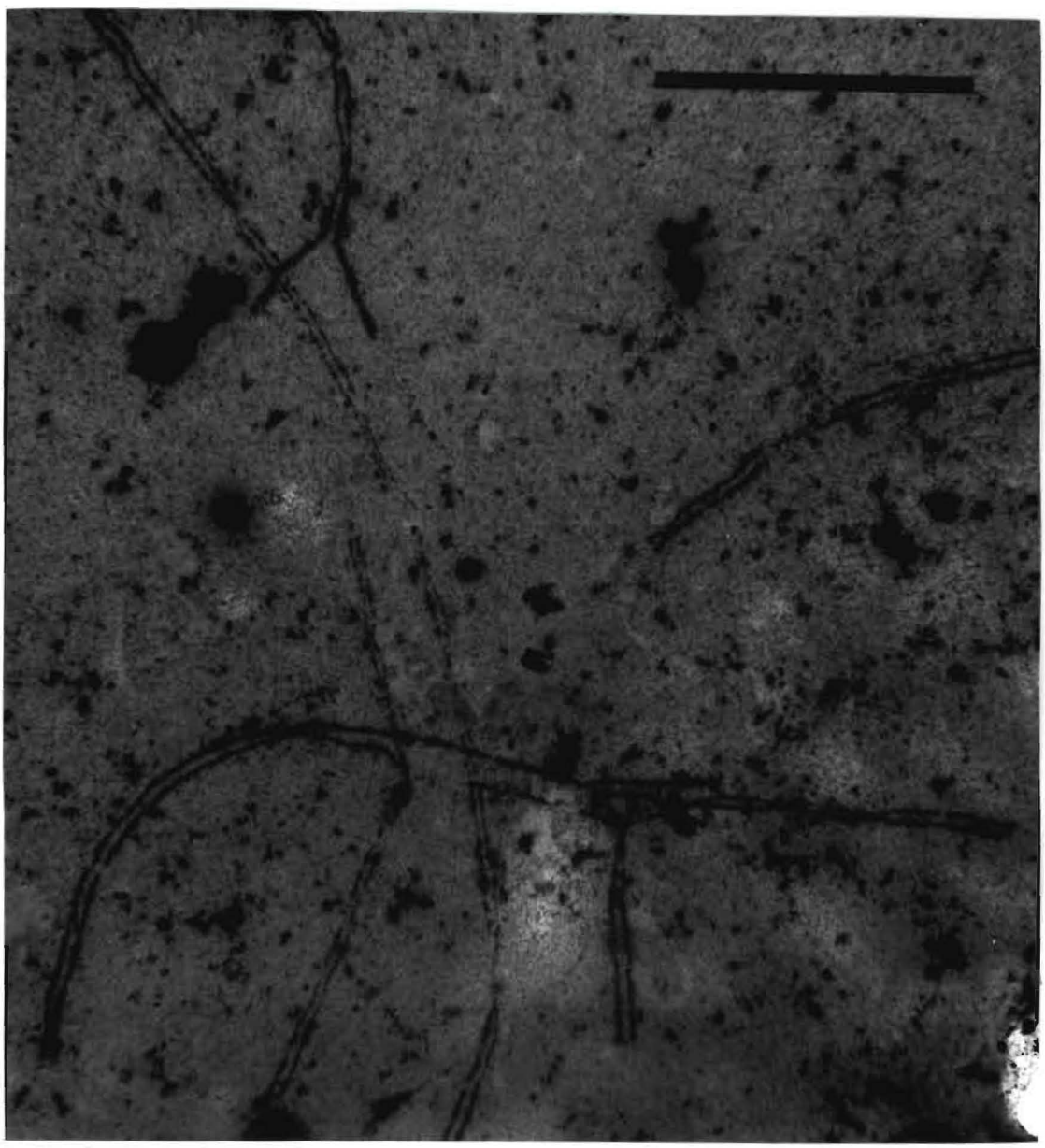
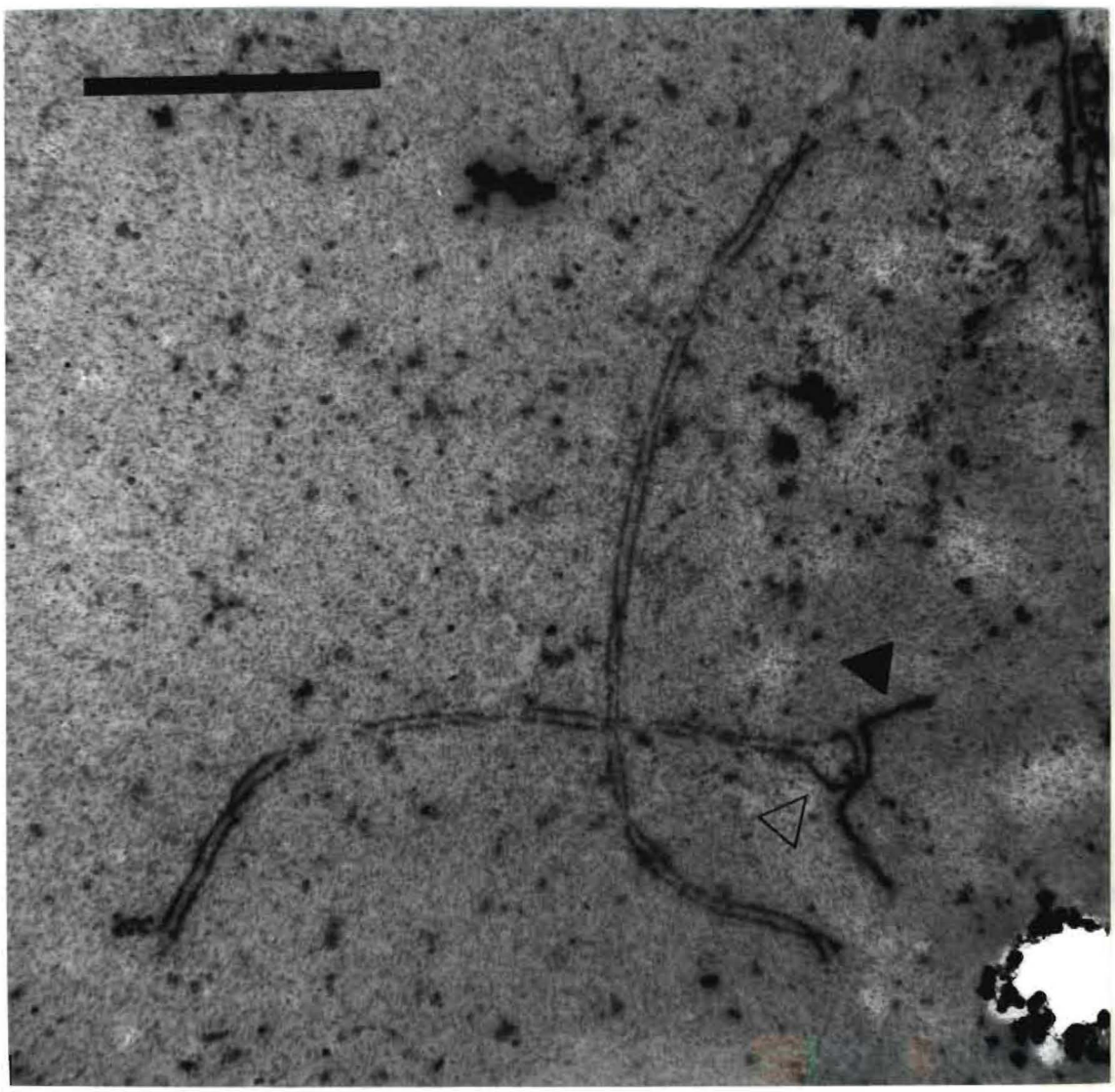


Fig. 8. Early pachytene silver-stained spread of northeastern individual showing incomplete pairing (solid arrow) and a buckle (open arrow) at one end. Bar represents 5 μm.



Discussion

Within the genus Peromyscus there are a number of species that differ by chromosomes that have inverted regions relative to each other. It has been thought that inversions represent a mechanism that prevents hybridization between many species of plants (McClintock, 1931,1933) and animals (Ehrman, 1962; Dobzhansky, 1970). Further studies of Peromyscus showed that some individual species carried, within their gene pools, the types of inversions that were seen, in other genera, as differences between species (Baker, 1983). The question therefore arises; how do populations of these species manage to maintain these different chromosomes in the heterozygous condition and still produce fertile offspring? Possibly there is a difference in chromosome pairing behaviors in meiosis between hybrids formed from parents from within a zone of contact and hybrids from parents out of the contact zone. Within the contact zone, selection may have acted to reduce the effects of the inversion on the hybrids. Selection, presumably, would not have had a chance to reduce the effects of the inversions in hybrids produced from parents outside of the zone of contact.

The successful breeding of lab-produced hybrid pairs showed that hybrid infertility does not result from the three pericentric inversions observed between the two

cytotypes of this species. However reproduction in the laboratory, where animals are kept in close proximity and are not given a choice of reproductive partners, is no proof that this hybrid mating occurs in nature. While it is possible that the hybrids may not as readily mate in the wild as they have done in the artificial laboratory situation, I have established that the production of offspring is possible between hybrids and that hybrids are certainly readily produced within the contact zone in Oklahoma.

Turning to the cytologic evidence we can gain further insights as to why this reproduction is possible. There seems to be no difference in the pairing mechanisms of chromosomes of hybrids produced within the hybrid zone of contact in Oklahoma and the pairing of chromosomes in lab-produced hybrids from parental types not likely to come into contact. Therefore, I conclude that this hybrid fertility is not the result of an adaptive mechanism that is unique to individuals within the zone of contact, but one which is inherent within the species itself. Inversions do not appear to provide a post-mating isolating mechanism in P. leucopus. Also, selection has not reduced hybrid infertility within the zone of contact, as hybrid infertility, apparently, is not a problem.

Heterosynapsis has been proposed to result from synaptic adjustment during the latter stages of pachytene,

as was shown by experiments with laboratory mice heterozygous for induced chromosomal rearrangements (Moses, 1977a; Moses et al., 1978; Ashley et al., 1981; Davisson et al., 1981; Moses and Poorman, 1981; Poorman et al., 1981a,b; Moses et al., 1982). Synaptic adjustment occurs in the later stages of pachytene, following the completion of homologous synapsis, which occurs in late zygotene and early pachytene. However, in this study heterosynapsis was observed in late zygotene and throughout pachytene, without asynapsis of chromosomes or formation of inversion loops. While failure to form an inversion loop has been reported previously (McClintock, 1931; Martin, 1967; Maguire, 1966) it was attributed to "topological limitations" resulting from the relatively small size of the chromosome involved (Ashley et al., 1981). However, at least one of the chromosomes involved in this study, chromosome number 5, is relatively large, and the inverted region constitutes approximately 40% of the chromosome. Nevertheless, inversion loops were not apparent in any stage. Hence I must assume heterosynapsis of chromosomes throughout the stages of meiosis I.

This phenomenon of heterosynapsis was first reported in 1986 by two independent researchers. Ashley and Russell (1986) termed this type of synapsis, which competes with homologous synapsis during zygotene and early pachytene, "G-synapsis", because the location of translocation

breakpoints with respect to the position of the G-bands in the sand rat (Psammomys obesus) were shown to have an important influence on the synaptic behavior of the translocations. If both breakpoints lie in G-light bands, synapsis will be restricted to homology, but if one of the breaks lies in a G-dark band, or very close to one, heterosynapsis can occur. Similar findings were reported as a result of a synaptonemal complex protein study on heterochromatin in species of Gerbillidae (Ratomponirina et al., 1986). This study indicates not only that the location of the point of breakage relative to heterochromatin on the chromosome may influence synapsis of nonhomologous chromosomes, but also that the presence of heterochromatin within translocated areas of the chromosomes may be necessary to maintain fertility. Heterosynapsis, also termed "straight pairing" has also been reported in the Sitka deer mouse (Peromyscus sitkensis) (Hale, 1986), in the deer mouse (Peromyscus maniculatus) (Greenbaum and Reed, 1984; Hale and Greenbaum, 1988), and in humans (Chandley et al., 1987). It has been hypothesized that the loss of the requirement for homology and the resultant heterosynapsed, straight-paired bivalent provides a conformation which is more stable than one consisting of reverse loops, duplication buckles, asynapsed regions, or length inequalities (Moses and Poorman, 1981; Moses et al., 1982).

While the configuration of heterosynapsed chromosomes

may provide more stability to the genome, some mechanism must then exist to inhibit the crossing over within non-homologous regions of the paired chromosomes to obviate the effects of deletions and duplications that would arise in the gametes if crossing over occurred. While this mechanism is not yet known, several possibilities present themselves. Again, the location of heterochromatin adjacent to inversions and translocations may have an effect on the frequency of crossing over. In addition, some genes are more prone to rearrangement and recombination than others, and these rearrangements are thought to be a function of gene expression (Smith, 1966; Sheldon et al., 1969). Thus, by changing the location of the gene on the chromosome, position effects may alter the genetic expression of recombination frequency. In this way inversions and translocations may cause some genes to increase, and others to decrease the frequency of crossing over. Alternatively, Ohno (1970) suggested that a difference in the density of heterosynapsed regions, as in the XY pair, minimizes crossing over between chromosomes.

A decreased mean number of chiasmata in heterokaryotypic bivalents has been observed in domestic chickens (Gallus domesticus) (Pollock and Fechheimer, 1977), suggesting that crossing over did not occur. Surprisingly, fertility of heterokaryotypic birds and the hatchability of the progeny were as high or higher than those of normal

birds (Dinkel et al., 1979). Thus, perhaps some mechanism within the chromosome itself discourages the crossing-over of nonhomologous chromosomes, and the maintenance of these chromosomal changes in the genome may increase the fitness of the population .

Furthermore, the maintenance of chromosomal changes in the gene pool may be more advantageous for some genera than for others. The genus Peromyscus carries within its gene pool a large number of inversions and heterochromatic additions. It is possible, therefore, that heterosynapsis is a generic trait. This trait may, by stabilizing the genome, decrease the genetic variation in the genus. It has been hypothesized that those genera with higher levels of recombination tend to be larger, slower developing, and to produce fewer young (Sharp et al., 1988). Genera that have a high rate of reproduction and therefore a high rate of population turnover in a short time, according to the hypothesis, would have fewer chiasma, and presumably less crossing over. Because the rate of turnover in the population is so high, the amount of genetic variation in each generation would be less essential than it would be in a population of large, slow-developing animals which have a low rate of reproduction and low population turnover. Therefore, the stable genome, maintained by heterosynapsis and the lack of crossing-over, could be advantageous for small rodents such as Peromyscus.

Summary

There seems to be no reduction in hybrid fertility due to pericentric inversions in the hybrid populations; either in the wild or in the laboratory. Fertility is maintained by heterosynaptic pairing of chromosomes within the inverted regions, while some unknown mechanism discourages crossing-over within the non-homologous regions, preventing duplications and deletions. It is possible that position effects of genes discourage crossing-over within the inverted regions, particularly when inversion breaks occur near non-coding heterochromatin regions. Hybrid fertility is not the result of an adaptive mechanism that is unique to individuals within the zone of contact, but one which is inherent within the species itself. The presence of a hybrid zone in Kansas is not prevented by pre- or post-mating isolating mechanisms, and pericentric inversions are not a factor in the evolution of subspecies within the species Peromyscus.

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PERICENTRIC INVERSIONS AS A REPRODUCTIVE ISOLATING MECHANISM IN DEER MICE (PEROMYSCUS LEUCOPUS)
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