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An assessment of the nature of chromosomal rearrangements in 18 species of *Peromyscus* (Rodentia: Cricetidae)

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Abstract. G- and C-banded karyotypes from 9 previously unstudied species of *Peromyscus* are described and compared to the 9 species described in the literature. Additional new data are presented for *P. eremicus*. A hypothetical evolutionary tree for the 18 species was constructed based on the assumption that, where possible, shared chromosomal rearrangements became established in a common ancestor. A minimum of 60 chromosomal rearrangements (34 heterochromatic additions and 26 pericentric inversions) were needed to construct the most parsimonious tree. Seven of the 18 species have heterochromatin in noncentromeric areas. Three times as many inversions have been identified in the 11 largest pairs as have been observed in the 12 smallest pairs. Peromyscine rodents are characterized by a pattern of chromosomal variation quite distinct from that described for other rodent genera, such as *Sigmodon* and *Mus*. Karyotypic orthoselection in rodents appears to be relatively common in closely related species.

From a cytogenetic viewpoint, mice of the genus *Peromyscus* have several aspects which make them of interest: the genus contains 59 species, many of which are easily obtainable from natural populations; laboratory colonies are easily established and maintained, as are primary tissue cultures of fibroblasts; and many species have a high

reproductive rate. Additionally, all species thus far examined have a diploid number of 48, but there is considerable intra- and inter-specific variation (HSU and ARRIGHI, 1968; TE and DAWSON, 1971; BOWERS et al., 1973; GREENBAUM et al., 1978a) in the number of acrocentrics versus biarmed elements. That *Cytogenetics and Cell Genetics* has published a standard G-band karyotype (COMMITTEE FOR STANDARDIZATION OF CHROMOSOMES OF *Peromyscus*, 1977) to be used in cytogenetic studies of the genus is further documentation of the level of interest and anticipation of further studies of *Peromyscus*.

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This report is concerned with determining the nature and extent of chromosomal rearrangements found in the 18 species for which there are G- and C-band data. We present G- and C-band data from *P. attwateri*, *P. boylii*, *P. californicus*, *P. difficilis*, *P. eremicus*, *P. leucopus*, *P. merriami*, *P. ochraventer*, *P. pectoralis*, and *P. truei*. Chromosomal data for *P. boylii* (COMMITTEE FOR STANDARDIZATION OF CHROMOSOMES OF *Peromyscus*, 1977) are presented as the standard. ARRIGHI et al. (1976) presented G- and C-band data for *P. leucopus*; however, we found it difficult to determine homologies for most of the smaller elements, and because *P. leucopus* has not been included in any of the previous studies of chromosomal homologies in *Peromyscus*, we include it in our comparisons. Chromosomal homology as related to the standard karyotype for *Peromyscus* (COMMITTEE FOR STANDARDIZATION OF CHROMOSOMES OF *Peromyscus*, 1977) is based on the following: *P. crinitus* (PATHAK et al., 1973; ARRIGHI et al., 1976), *P. alstoni* (YATES et al., 1979), *P. gossypinus* and *P. floridanus* (GREENBAUM and BAKER, 1978), *P. polionotus* (GREENBAUM et al., 1978b), *P. maniculatus* and *P. melanotus* (GREENBAUM et al., 1978a), and *P. oreas* (BAKER et al., 1981). There is also extensive data available from studies of chromosomal homology between species of *Peromyscus* and representatives of *Neotoma* (MASCARELLO et al., 1974), *Onychomys* (BAKER et al., 1979; BAKER and BARNETT, 1981), *Baiomys* (YATES et al., 1979), and *Reithrodontomys* (ROBBINS and BAKER, 1980). These data have been interpreted as indicating that the karyotype for the common ancestor of all *Peromyscus* species contained heterochromatin only in the centromeric regions, elements 1, 22, and 23 were biarmed with euchromatic short

arms, and all other autosomal elements were acrocentric. We have used this "proposed primitive" condition as the base for an evolutionary tree to be used for detecting patterns and direction of chromosomal change in *Peromyscus*.

Materials and methods

G- and C-band preparations for *P. difficilis*, *P. ochraventer*, and *P. pectoralis* were obtained from fibroblast tissue cultures initiated from ear biopsies, as described by GREENBAUM et al. (1978a). G- and C-band preparations for *P. attwateri*, *P. boylii*, *P. californicus*, *P. eremicus*, *P. leucopus*, *P. merriami*, and *P. truei* were obtained by the standard bone marrow technique, as modified by LEE and ELDER (1980). All specimens were from natural populations. Standard karyotypes were examined for all specimens. Illustrated in fig. 1 is a haploid autosomal complement of eight species of *Peromyscus* (*P. boylii*, *P. californicus*, *P. attwateri*, *P. difficilis*, *P. pectoralis*, *P. ochraventer*, *P. truei*, and *P. leucopus*). The X chromosomes from all species and the Y chromosomes from *P. attwateri*, *P. pectoralis*, and *P. truei* are illustrated at the lower right corner of fig. 1b. The G-bands of chromosome pair 6 of *P. eremicus* and *P. merriami* are shown in fig. 2.

Any rearrangement that changes an acrocentric chromosome into a biarmed chromosome with euchromatic short arms is considered to be a pericentric inversion (ARRIGHI et al., 1976) if the G-band pattern shows positive correlation or does not refute this assumption. If the short arms stain positive for heterochromatin (fig. 3), and the G-band pattern on the long arm remains, as in the proposed primitive karyotype, a heterochromatic addition is assumed (PATHAK et al., 1973). Faint G-bands can be seen in some C-band preparations, allowing for a more accurate determination of homologies.

Species are grouped in fig. 4 based on the assumptions that shared chromosomal rearrangements became established in a common ancestor, and that the most parsimonious positioning of rearrangements, using the above criteria, would pro-

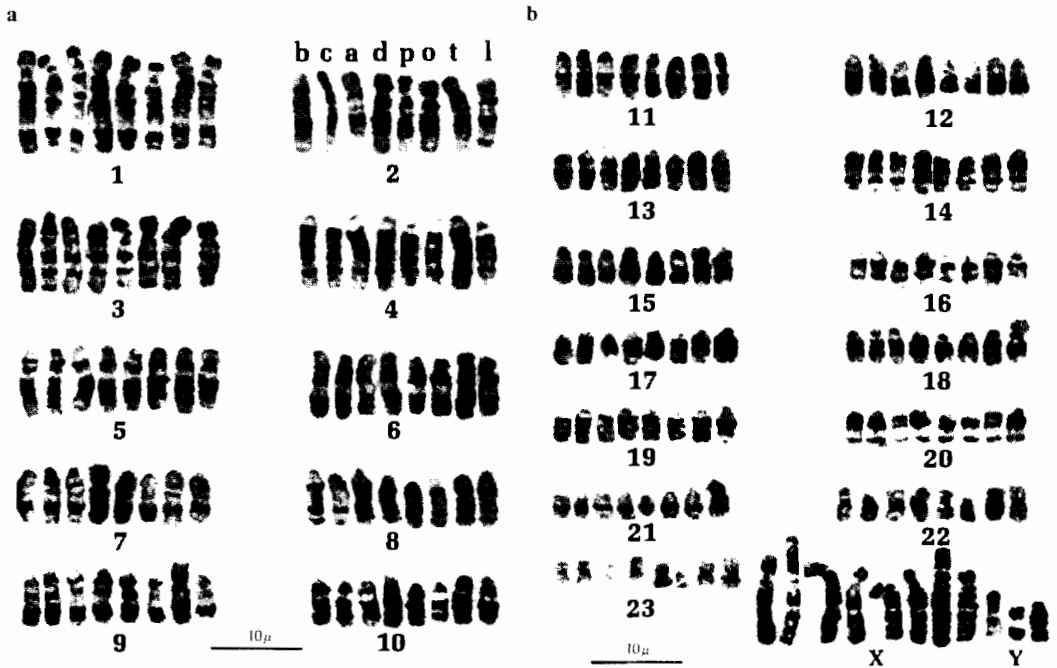


Fig. 1. Composite autosomal G-banded haploid karyotypes, each from a single diploid cell, of *Peromyscus boylii*, *P. californicus*, *P. attwateri*, *P. difficilis*, *P. pectoralis*, *P. ochraventer*, *P. truei*, and *P. leucopus*, from left to right respectively. Chromosomes are numbered according to proposed homology to the standard *Peromyscus* karyotype (COMMITTEE FOR STANDARDIZATION OF CHROMOSOMES OF *Peromyscus*, 1977). **a.** Chromosomes 1 through 10. **b.** Chromosomes 11 through 23, plus the X chromosomes from all species and the Y chromosomes from *P. attwateri*, *P. pectoralis*, and *P. truei*, from left to right.

vide the most probable evolutionary tree for the 18 species. It should be noted that the 18 species could not be placed in a "tree" where all shared chromosomal rearrangements could be explained as evolving only once. These rearrangements are denoted by an asterisk. For some chromosomes, the location of the rearrangement on the tree is arbitrary; however, such variation in placement would not alter the branching sequence shown in fig. 4 without requiring more rearrangements. Rearrangements which occur as polymorphisms or as regional characteristics of a population are shown in parentheses.

Specimens examined

G-bands were examined from all specimens listed below, and C-bands from each species. *P. attwateri* (7) Texas: Garza Co.; 10 mi S Post (3

males, 4 females). *P. boylii* (1) New Mexico: Socorro Co.; 32 mi S, 19.5 mi W Socorro (1 female). *P. californicus* (6) California: Alameda Co.; Russel Reservation, Lafayette (1 female); Contra Costa Co.; Clarmont Canyon (2 males, 1 female); San Bernardino Co.; 2 mi N, 7 mi E Mentone (2 females). *P. difficilis* (1) Mexico: Durango; 18 mi W El Salto (1 female). *P. eremicus* (3) Arizona: Cochise Co.; 2 mi SE Portal (2 males, 1 female). *P. leucopus* (3) Texas: Garza Co.; 14 mi NE Southland (1 male, 1 female); 10 mi S Post (1 male). *P. merriami* (7) Arizona: Pima Co.; 12 mi S Tucson, Santa Cruz River (3 males, 4 females). *P. ochraventer* (1) Mexico: San Luis Potosi; 25 mi W Ciudad Valles (1 female). *P. pectoralis* (3) Texas: Kimble Co.; 1 mi S Junction (1 female). Mexico: Coahuila; 30 mi E Parras (1 male); Durango; 35 mi SW Gomez Palacio (1 female). *P.*

truei (11) New Mexico: Socorro Co.; 2 mi S, 23.5 mi W Socorro (1 male); Sandoval Co.; 4 mi S, 31 mi W Bernalillo (1 male, 2 females); Texas: Briscoe Co.; 6 mi N, 4 mi W Silverton (4 males, 3 females).

Results

P. attwateri ($2n = 48$, FN = 56). All autosomes are acrocentric except pairs 1, 2, 6, 22, and 23. Heterochromatin is restricted to the centromeric regions.

P. boylii ($2n = 48$, FN = 52). All autosomes are acrocentric except pairs 1, 22, and 23. Heterochromatin is restricted to the centromeric regions. Our G- and C-banded karyotypes of this specimen are like those reported as the standard for *Peromyscus* (COMMITTEE FOR STANDARDIZATION OF CHROMOSOMES OF *Peromyscus*, 1977) and resemble the chromosomal race from the United States and northern Mexico (SCHMIDLY and SCHROETER, 1974). It is included here as an example of the proposed primitive condition, with all others being compared to this standard.

P. californicus ($2n = 48$, FN = 54). All autosomes are acrocentric except pairs 1, 2, 22, and 23. Heterochromatin is restricted to the centromeric regions.

P. difficilis ($2n = 48$, FN = 58). All autosomes are acrocentric except pairs 1, 2, 6, 7, 22, and 23. Heterochromatin is restricted to the centromeric regions. LEE et al. (1972) examined the karyotypes of 20 specimens that agree with the one described in this paper; however, HSU and ARRIGHI (1968) described the karyotype of this species as having an FN = 56.

P. eremicus ($2n = 48$, FN = 96). All autosomes are biarmed. Pairs 1 and 23 have entirely euchromatic short arms. Pairs 6 and



Fig. 2. G-banded chromosome 6 from *Peromyscus eremicus* (pair on left) and *P. merriami*.

22 have telomeric heterochromatin on the short arms, and all other pairs have heterochromatic short arms. Figure 2 illustrates that the euchromatic portion of the short arm of chromosome 6 is the result of a pericentric inversion.

P. leucopus ($2n = 48$, FN = 70). All autosomes are acrocentric except pairs 1, 2, 3, 5, 6, 9, 11, 12, 18, 21, 22, and 23. Of these biarmed elements, pairs 1, 2, 3, 5, 6, and 9 have short arms that are entirely euchromatic (fig. 3), and pair 12 has short arms that are entirely heterochromatic. Pairs 11, 18, 21, 22, and 23 have short arms composed of proximal euchromatic and distal heterochromatic segments. In pairs 22 and 23 there are the euchromatic biarmed segments that are found in all species of the genus plus heterochromatic additions. In pairs 11, 18, and 21 the euchromatic segment found in the small arms may have been the result of pericentric inversions and/or nucleolar organizing regions between the centromere and the heterochromatic region. The interstitial bands seen in pairs 1, 2, 4, and 7 were noted by ARRIGHI et al. (1976). Only the heterochromatic band seen in chromosome 2 (fig. 3) was found consistently in all spreads. This band is shown in fig. 1a as the additional band near the distal end of the *P. leucopus* chromosome 2. It appears to be a character unique to this species.

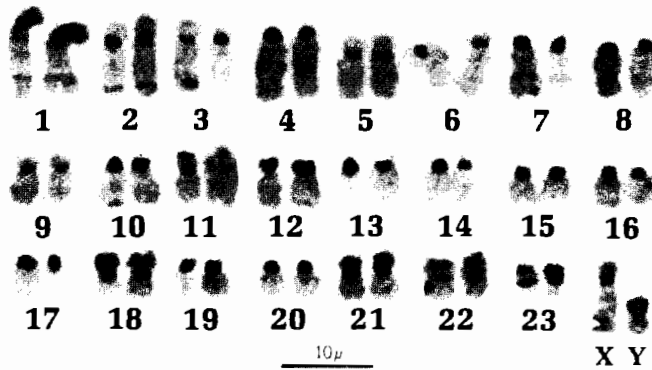


Fig. 3. C-banded karyotype of *Peromyscus leucopus*.

P. merriami ($2n = 48$, FN = 96). All autosomes are biarmed. Pairs 1, 6, and 23 have entirely euchromatic short arms, pair 22 has telomeric heterochromatin on the short arms, and all other pairs have heterochromatic short arms. The short arm of chromosome 6 is a result of a pericentric inversion; however, the banding pattern and centromere placement indicate a different inversion than that seen in *P. eremicus* (fig. 2).

P. ochraventer ($2n = 48$, FN = 60). All autosomes are acrocentric except pairs 1, 2, 3, 6, 9, 22, and 23. Heterochromatin is restricted to the centromeric regions.

P. pectoralis ($2n = 48$, FN = 58). All autosomes are acrocentric except pairs 1, 2, 3, 9, 22, and 23. Heterochromatin is restricted to the centromeric regions. Specimens from the United States and Mexico have identical banding patterns.

P. truei ($2n = 48$, FN = 62). All autosomes are acrocentric except pairs 1, 2, 3, 6, 9, 15, 22, and 23. Heterochromatin is restricted to the centromeric regions. Pair 1 has undergone an inversion, so that the short arm is longer and has acquired an extra band. This is the only species thus far examined that has an acrocentric Y chromosome.

Discussion

A minimum of 60 independent chromosome rearrangements (34 heterochromatic additions and 26 pericentric inversions) are needed to construct the most parsimonious "tree" (fig. 4) from the proposed primitive karyotype for the genus. One species, *P. crinitus*, has a karyotype which does not vary from the proposed primitive one. *P. boylii* also has a karyotype like the proposed primitive; however, *P. boylii* has an established polymorphism in pair 9 (GREENBAUM and BAKER, 1978).

Heterochromatic additions. Of the 34 heterochromatic additions detected thus far, 21 occur in the *P. eremicus* (*eremicus* and *merriami*) species group. One inversion has also been detected in each of these species (fig. 3). All other heterochromatic additions are found in the *P. leucopus* (*leucopus* and *gossypinus*) and *P. maniculatus* (*maniculatus*, *polionotus*, and *oreas*) species groups. Of the nine species thus far examined from these three species groups, only *P. melanotis* has heterochromatin restricted to the centromeric regions. Interstitial heterochromatin for members of the genus has been detected

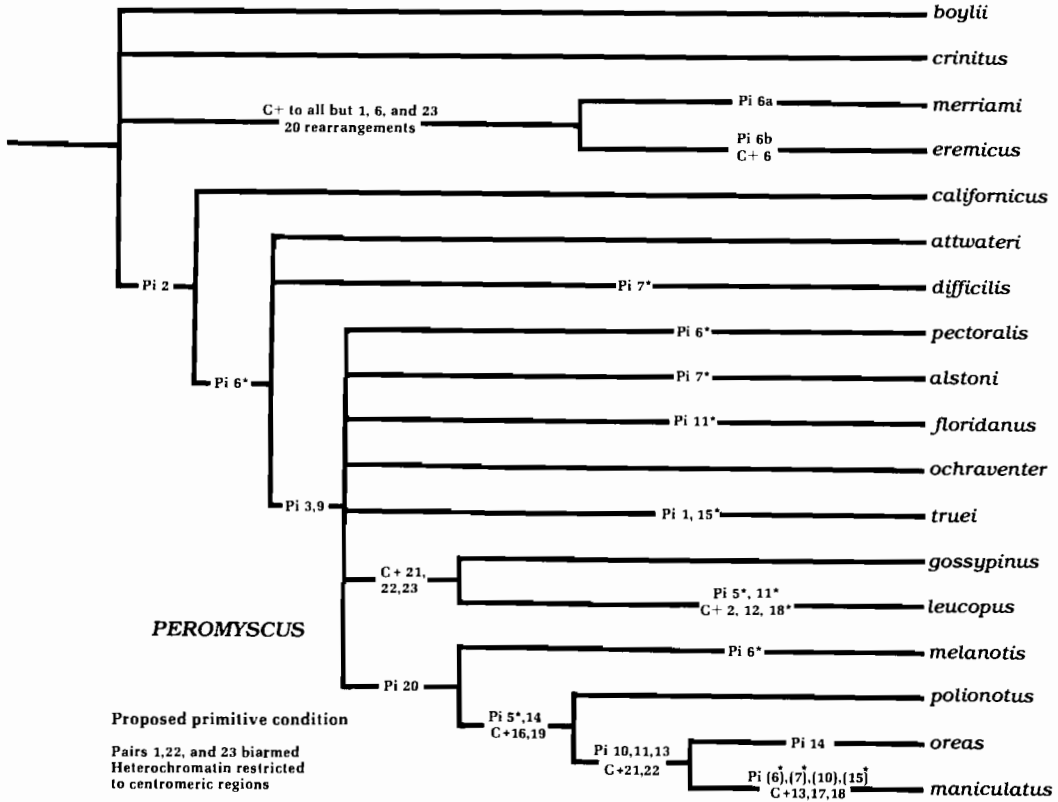


Fig. 4. Arrangement of 18 species of *Peromyscus* derived from an analysis of chromosomal homology based on G- and C-bands. Pi = pericentric inversion and C+ = heterochromatic addition. See materials and methods section for an explanation of the numbers in parentheses and the rearrangements marked by an asterisk.

only in *P. leucopus*, which has such bands in pairs 1, 2, 4, and 7 (ARRIGHI et al., 1976, and fig. 3). Although a greater number of heterochromatic additions are found in the genus, only 7 of the 18 species studied herein have undergone such rearrangements.

Pericentric inversions. Chromosome pairs 1, 2, 3, 5, 6, 7, 9, 10, 11, 13, 14, 15, and 20 have been inverted in one or more species from the proposed primitive condition (fig. 4). Of the 18 species studied, 16 have one or more chromosomes inverted from the

proposed primitive condition. Although there have been fewer pericentric inversions (26, as compared to 34 heterochromatic additions) established in the genus, a greater percentage of the species sampled have undergone pericentric inversions.

If the frequency of multiple breaks on the same chromosome is the single most important factor in the establishment of pericentric inversions, and the probability of a break is roughly proportional to the length of a chromosome, then the larger elements

should be more frequently inverted than the smaller ones. Of the 11 largest pairs, only two (4 and 8) have not been rearranged. Additionally, pairs 5, 6, 7, and 11 have been rearranged more than once, for a minimal total number of 19 pericentric inversions. Pair 6 has been rearranged a minimum of six times and, although a high mutation rate has been noted for certain areas on specific human chromosomes (AURIAS et al., 1978), further study is needed to determine if these are comparable phenomena or if the patterns we see in *Peromyscus* are the result of selection pressures. Of the smallest 12 pairs, 8 (12, 16, 17, 18, 19, 21, 22, and 23) do not appear to have been rearranged, and only 2 (14 and 15) were rearranged twice. This results in a minimal total of six pericentric inversions in the 12 smallest pairs. Thus, over three times as many pericentric inversions have been detected in the larger elements than in the smaller elements, which is compatible with the hypothesis that the frequency of rearrangement is a function of the size of the chromosome. Although it might be argued that rearrangements are less easily detected in smaller elements and that the magnitude of the difference may to some extent be technical in nature, this would not be true for pericentric inversions, because the biarmed condition is easily distinguished from the acrocentric.

One of the more interesting cytogenetic features of peromyscine rodents is their extreme conservation of centromere numbers. Three peromyscine genera (*Onychomys*, *Baiomys*, and *Reithrodontomys*) other than *Peromyscus* have been studied by G- and C-banding techniques. In *Onychomys* (BAKER and BARNETT, 1981), all species have a $2n = 48$ with identical euchromatic segments in all three species (no inversions),

and each species varies from the others by heterochromatic short-arm additions. A total of 34 independent heterochromatic additions are hypothesized (BAKER and BARNETT, 1981) as occurring in the evolution of the genus. Of the euchromatic segments, all are identical to the proposed primitive karyotype for *Peromyscus* (fig. 4) except pairs 9 and 19, which have been inverted to the biarmed condition. In *Baiomys* (YATES et al., 1979), the diploid number of 48 is maintained in both species, and all euchromatic segments are identical to the proposed primitive karyotype for *Peromyscus* (fig. 4) except for inversions in pairs 1, 22, and 23. We have examined G- and C-bands of *B. musculus* chromosomes and found that they differ from those of *B. taylori* by the presence of heterochromatic additions. In *Reithrodontomys* (four species examined, ROBBINS and BAKER, 1980), one species (*R. fulvescens*) has maintained a $2n = 50$ with all euchromatic banding patterns proposed as primitive for *Peromyscus* except for inversions in chromosomes 1, 22, and 23, plus an additional pair of small chromosomes. Only in *Reithrodontomys* is there a radical departure from the conservation of the euchromatic segments and diploid number of 48. The most extreme examples were *Reithrodontomys montanus* ($2n = 38$) and *R. megalotis* ($2n = 42$), where not only has the diploid number been radically altered, but it was also not possible to identify a single euchromatic banding sequence homologous to any in the proposed primitive karyotype of *Peromyscus*.

In an overview of peromyscine rodents, we see minimal variation in diploid numbers, conservatism in the banding pattern for euchromatic linkage groups, and rearrangements which are primarily heterochromatic additions and pericentric inversions.

That pericentric inversions occur on a variety of elements is proof that breaks are happening in such places on the chromosomes that centric fusions should be possible. However, with the possible exception of *Reithrodontomys*, these fusions appear not to have occurred. What we can note with reasonable certainty is that enough peromyscine rodents have been studied karyotypically to conclude that centric fusions rarely occur in natural populations or in tissue-culture lines. Data from peromyscine rodents produce a uniquely different pattern than that reported for other rodent genera thus far studied. Chromosomal variations within the genus *Sigmodon* is characterized by tandem and centric fusions (ELDER, 1980). In the genus *Mus*, the Old World equivalent of *Peromyscus*, some species have maintained identical karyotypes (HSU et al., 1978), while in *M. musculus*, a minimum of 27 centric fusions have been established with no inversions or heterochromatic additions (CAPPANA et al., 1976). From these examples, one can see that the probability of such variations in frequency of certain types of rearrangements in rodents is not easily explained by stochastic processes, and karyotypic orthoselection, as defined by WHITE (1975), is not uncommon.

We are not able at this time to offer either a cytogenetic or a biological explanation that can easily explain the restricted rate of centric fusions in peromyscine rodents. In the two species in which the diploid number has been altered (*R. montanus* and *R. megalotis*), the integrity of the linkage groups has also been radically altered. At least superficially, it appears that there is strong selection for maintenance of the 24 linkage groups. Peromyscine rodents offer the combination of favorable experimental features and an array of unanswered cyto-

genetic questions. This group of rodents provide a fertile field which can challenge man's ability to design logical experiments that force nature to provide answers to such questions.

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