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Cytogenetic nomenclature of deer mice, *Peromyscus* (Rodentia): revision and review of the standardized karyotype

Report of the Committee for the Standardization of Chromosomes of *Peromyscus*

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Abstract. A revision of the standardized karyotype of deer mice (*Peromyscus*) is presented. This revision addresses shortcomings of the original standardization, contains a substantial increase in the number of G-band markers and provides a nomenclature for the G-bands of each autosome and the X chromosome. Using the revised standardized karyotype, we specify the particular G-bands or patterns that identify each chromo-

some and catalog the more problematic chromosome identifications and likely misidentifications. For each chromosome, we present an overview of previously reported variation in euchromatic arrangement and heterochromatic constitution. We then review previous applications of the standardized karyotype and summarize the predominant findings from cytogenetic and cytogenetic studies of *Peromyscus* and related taxa.

The development of "A Proposed Standard System of Nomenclature of Human Mitotic Chromosomes," generally known as the Denver Conference (1960), established the precedent for adopting consensus references aimed at eliminating confusion and improving communication among researchers

involved in cytogenetic studies of popular model organisms. The report of the Denver Conference served as the basis for subsequent reports which led to the current International System for Human Cytogenetic Nomenclature (ISCN, 1985) and provided a model for the development of similar systems for laboratory mice (Committee on Standardized Genetic Nomenclature for Mice, 1972), laboratory rats (Committee for a Standardized Karyotype of *Rattus norvegicus*, 1973) and domestic animals (ISCNDA, 1989). In each of these cases, the standardized chromosome nomenclature was designed to facilitate the identification of chromosomal conditions of single species.

A somewhat different situation exists for standardization of the chromosomes of mice of the North American genus, *Peromyscus*. In this case, the standardized karyotype (Committee for the Standardization of Chromosomes of *Peromyscus*, 1977)

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Table 1. List of the species of *Peromyscus* and phylogenetically allied rodents for which chromosome banding data have been previously published.

Taxon	G-band	C-band	Reference	Taxon	G-band	C-band	Reference
Genus <i>Peromyscus</i>				Genus <i>Peromyscus</i> (continued)			
<i>crinitus</i> group				<i>truei</i> group			
<i>crinitus</i>	X	X	Pathak et al. (1973)	<i>difficilis</i>	X	X	Robbins and Baker (1981)
	X	X	Arrighi et al. (1976)	<i>gratus</i>	X	X	Modi and Lee (1984)
		X	Hazen et al. (1977)	<i>truei</i>	X	X	Robbins and Baker (1981)
					X	X	Modi and Lee (1984)
<i>maniculatus</i> group				<i>melanophrys</i> group			
<i>maniculatus</i>	X	X	Bradshaw and Hsu (1972)	<i>melanophrys</i>	X	X	Zimmerman (1974)
	X	X	Duffey (1972)	<i>perfulvus</i>	X	X	Stangl and Baker (1984)
	X	X	Murray and Kitchin (1976)				
	X	X	Greenbaum et al. (1978a)	<i>mexicanus</i> group			
	X	X	Gunn and Greenbaum (1986)	<i>furnus</i>	X	X	Smith et al. (1986)
	X	X	Gunn (1988)	<i>guatemalensis</i>	X	X	Rogers et al. (1984)
	X	X	Greenbaum and Reed (1984)	<i>gymnotis</i>	X	X	Rogers et al. (1984)
	X	X	Hale and Greenbaum (1988a, b)	<i>megalops</i>	X	X	Smith et al. (1986)
	X	X	Hale et al. (1991)		X	X	Hale et al. (1991)
<i>melanotis</i>	X	X	Greenbaum et al. (1978a)	<i>melanurus</i>	X	X	Smith et al. (1986)
<i>polionotus</i>	X	X	Greenbaum et al. (1978b)	<i>mexicanus</i>	X	X	Rogers et al. (1984)
<i>oreas</i>	X	X	Gunn and Greenbaum (1986)	<i>nudipes</i>	X	X	Stangl and Baker (1984)
	X	X	Gunn (1988)	<i>ochraventer</i>	X	X	Robbins and Baker (1981)
<i>sitkensis</i>	X	X	Pengilly et al. (1983)	<i>yucatanicus</i>	X	X	Rogers et al. (1984)
	X	X	Greenbaum et al. (1986b)	<i>zachrychus</i>	X	X	Rogers et al. (1984)
	X	X	Hale and Greenbaum (1986)				
	X	X	Hale (1986)	<i>californicus</i> group			
	X	X	Hale and Greenbaum (1988a)	<i>californicus</i>	X	X	Robbins and Baker (1981)
	X	X	Hale et al. (1991)				
<i>leucopus</i> group				<i>eremicus</i> group			
<i>leucopus</i>	X	X	Arrighi et al. (1976)	<i>eremicus</i>	X	X	Pathak et al. (1973)
	X	X	Robbins and Baker (1981)		X	X	Arrighi et al. (1976)
	X	X	Baker et al. (1983)			X	Hazen et al. (1977)
	X	X	Stangl (1986)		X	X	Sudman and Greenbaum (1989)
	X	X	Stangl and Baker (1984)			X	Robbins and Baker (1981)
	X	X	Stangl and Baker (1989)			X	Hale et al. (1991)
	X	X	McBee (1991)	<i>collatus</i>		X	Hazen et al. (1977)
		X	Hale et al. (1991)	<i>merriami</i>	X	X	Robbins and Baker (1981)
<i>gossypinus</i>	X	X	Greenbaum and Baker (1978)	Genus (= subgenus?) <i>Habromys</i>			
				<i>lepturus</i>	X	X	Rogers et al. (1984)
<i>aztecus</i> group				Genus (= subgenus?) <i>Podomys</i>			
<i>aztecus</i>	X	X	Smith (1990)	<i>floridanus</i>	X	X	Greenbaum and Baker (1978)
		X	Hale et al. (1991)	Genus (= subgenus?) <i>Neotomodon</i>			
<i>evides</i> ¹	X	X	Smith (1990)	<i>alstoni</i>	X	X	Yates et al. (1979)
<i>hylocetes</i> ¹	X	X	Smith (1990)	Genus (= subgenus?) <i>Megadontomys</i>			
<i>oaxacensis</i> ¹	X	X	Smith (1990)	<i>cryophilus</i>	X	X	Rogers (1983) ³
<i>spicilegus</i>	X	X	Smith (1990)	Genus (= subgenus?) <i>Osgoodomys</i>			
<i>winkelmanni</i>	X	X	Smith (1990)	<i>banderanus</i>	X	X	Rogers et al. (1984)
<i>boylly</i> group				Genus (= subgenus?) <i>Isthmomys</i>			
<i>atwatteri</i>	X	X	Robbins and Baker (1981)	<i>pirrensis</i>	X	X	Stangl and Baker (1984)
<i>beatae</i>	X	X	Davis et al. (1986) ²				
	X	X	Houseal (1987)				
		X	Sudman and Greenbaum (1989, 1990)				
		X	Sudman et al. (1989)				
	X	X	Smith (1990)				
<i>boylly</i>	X	X	Committee (1977)				
	X	X	Robbins and Baker (1981)				
	X	X	Smith et al. (1986)				
	X	X	Smith (1990)				
<i>levipes</i>	X	X	Smith (1990)				
<i>pectoralis</i>	X	X	Robbins and Baker (1981)				
	X	X	Smith (1990)				
<i>stephani</i>		X	Hazen et al. (1977)				

¹ These taxa have alternatively been considered as species (Hooper, 1968) or as subspecies of *P. aztecus* (Carleton, 1989).

² These specimens were reported as *P. boylly*. Identification of these populations as *P. beatae* is discussed in Rennert and Kilpatrick (1987), Houseal et al. (1987) and Schmidly et al. (1988).

³ These specimens were reported as *P. thomasi cryophilus*. Carleton (1989) recognized this taxon as specifically distinct.

has provided a system of nomenclature for the chromosomes of the array of species of *Peromyscus* and closely related genera. The genus *Peromyscus* includes over 50 species (Carleton, 1989) whose combined geographic distribution extends from the Atlantic to the Pacific coasts and from the Canadian

subarctic to Panama. One or more species of *Peromyscus* occur in nearly every terrestrial habitat in North America. Deer mice have long been the subject of research in areas ranging from behavior, ecology and physiology to molecular biology and cytogenetics. The significance of *Peromyscus* to systematic

mammalogy has been compared to that of *Drosophila* in the growth of systematic biology as a whole (Carleton, 1989). To this end, studies of the cytogenetics of *Peromyscus* have been particularly informative. With recent advances in cytogenetic and molecular technology, studies involving the chromosomes of *Peromyscus* and related taxa are likely to increase in both popularity and importance.

Early karyological studies indicated that species of *Peromyscus* have a karyotype comprised of 23 autosomal pairs and the sex pair. Among species, however, there is extensive variation in number of autosomal arms (fundamental number, FN) and in the morphologies of the X and Y chromosomes. Descriptive G- and C-banded chromosome data have been published for over 40 species of *Peromyscus* (Table I). Analyses of chromosome banding data indicate that chromosome differences among species of these rodents result primarily from pericentric inversions and addition/deletion of constitutive heterochromatin. These types of chromosome rearrangements also occur as polymorphisms within some species of *Peromyscus* (Greenbaum et al., 1978a, b; Baker et al., 1983; Pengilly et al., 1983; Greenbaum and Reed, 1984; Davis et al., 1986; Gunn and Greenbaum, 1986; Hale, 1986; Stangl, 1986; Gunn, 1988; Hale and Greenbaum, 1988a, b; Stangl and Baker, 1989; Smith, 1990; Sudman and Greenbaum, 1990). In nearly all cases, the pericentric inversions have involved terminal segments and have resulted in alternative acrocentric and biarmed (metacentric and submetacentric) chromosome morphologies.

The centromeric regions of deer-mouse chromosomes are typically C-band positive, although at least one species (*P. polionotus*) possesses some chromosomes with centromeric regions which are noticeably less C-band positive (Greenbaum et al., 1978b). Among, and in some cases within, species of *Peromyscus*, the length of an autosome can be affected by the presence of noncentromeric heterochromatin. Noncentromeric heterochromatin may comprise an entire chromosome arm, a terminal region distal to the end of an otherwise euchromatic arm or, less frequently, an interstitial region.

The standardized karyotype of *Peromyscus* (Committee for the Standardization of Chromosomes of *Peromyscus*, 1977) has provided the system for description and identification of the chromosome differentiation among and variation within species. This system facilitated comparisons of the data and analyses of chromosome evolution and systematics of deer mice (Greenbaum et al., 1978b; Greenbaum and Baker, 1978; Yates et al., 1979; Robbins and Baker, 1981; Rogers, 1983; Rogers et al., 1984; Stangl and Baker, 1984; Smith, 1990). However, the 1977 standardization contains problems in its application and does not provide a system for identifying landmarks on individual chromosomes. Further advances in the cytogenetics of *Peromyscus* are critically dependent on an appropriate revision and improvement of the standardized karyotype of deer mice. In particular, a G-band nomenclature is necessary for the development of genetic maps for *Peromyscus*. Genetic-map information is currently available for 28 species of mammals (O'Brien, 1990) and eight linkage groups have been identified for *Peromyscus* (Dawson and Rogers, 1993). The availability of a large number of cDNA clones for *Mus* (Eppig, 1992) and technical developments in fluorescence in situ hybridization should

permit the physical mapping of genes on the chromosomes of *Peromyscus*. With an enhanced cytogenetic nomenclature, the available technology will enable the chromosome assignment of linkage groups and facilitate evolutionary analyses of comparative gene maps.

The present effort was designed to: (1) identify and minimize problems in the 1977 standardized karyotype; (2) improve resolution of the standardized karyotype; (3) develop a nomenclature which allows identification of landmarks on the numbered, G-banded chromosomes; and (4) present an overview of the use of the standardized karyotype of deer mice and its applications to cytogenetic research on *Peromyscus* and allied species.

Chromosome nomenclature

The 1977 standardized karyotype of *Peromyscus* was based on G-banded chromosome data from four specimens of *P. boylii glasselli* (from Isla San Pedro Nolasco in the Gulf of California). For this report, we critically compared all published G- and C-banded chromosome data for *Peromyscus*. Where possible, original data (negatives or photographs) were used for these comparisons. Additionally, over 100 unpublished G- and C-banded karyotypes (mostly from *P. maniculatus*) were analyzed and compared.

The karyotype used for the original standardization (FN = 52) appears to represent the "primitive" condition for *Peromyscus* (Greenbaum and Baker, 1978; Yates et al., 1979; Robbins and Baker, 1981; Rogers et al., 1984; for review see Carleton, 1989). This FN = 52 karyotype has only three biarmed chromosomes (Chr 1, 22 and 23) and autosomal heterochromatin restricted to the centromeric regions. We have retained this karyotype as the basis for the revision. The FN = 52 version of the revised and annotated ideogram for the standardized karyotype for *Peromyscus* is presented in Fig. 1.

The revised standardized karyotype of *Peromyscus* maintains most of the chromosomal numbering assigned in the 1977 standardization. In general, the autosomes are arranged and numbered according to their euchromatic length. Chromosomes 22 and 23, which are generally biarmed with both arms euchromatic, were retained as the last two autosomal pairs. The numbering of the chromosomes in the revision is not, however, identical to that of the 1977 standardization. Comparisons of the published G-banded karyotypes of *Peromyscus* indicated ambiguity in the identification of some autosomes. These problems appear to have resulted from: inconsistencies between the ideogram and the G-banded karyotypes in the 1977 standardization; inconsistencies between the two G-banded karyotypes in the 1977 standardization; and errors in the original ideogram. The quantity and improved quality of G-banded chromosomal data now available have enabled us to generate the revised standardized ideogram (Fig. 1) and corresponding G-banded karyotype (Fig. 2) for *Peromyscus*. A key to the changes in the numbering of the autosomes is presented in Table II.

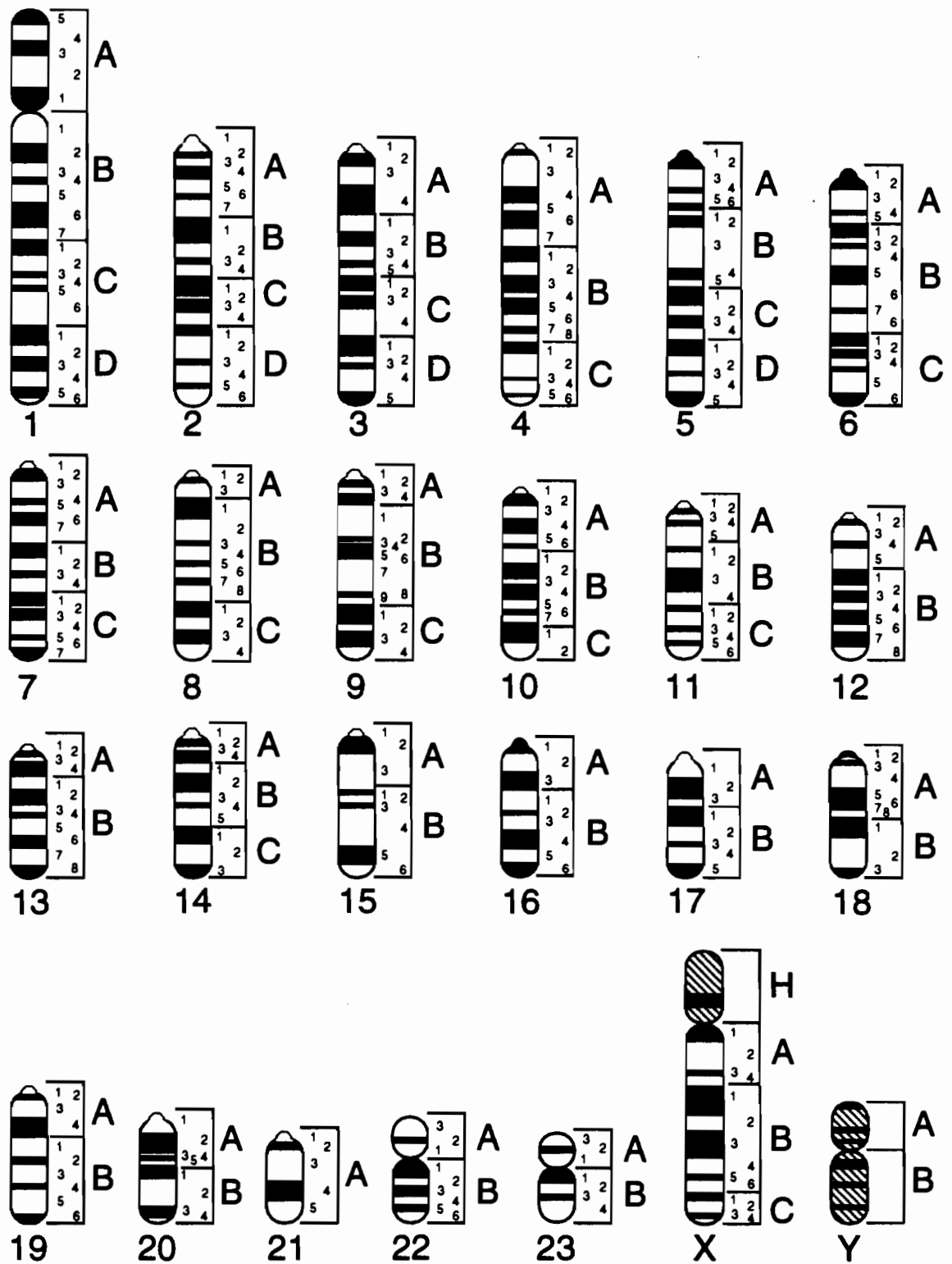


Fig. 1. Revised ideogram of the G-banding pattern for the FN = 52 karyotype of *Peromyscus*.

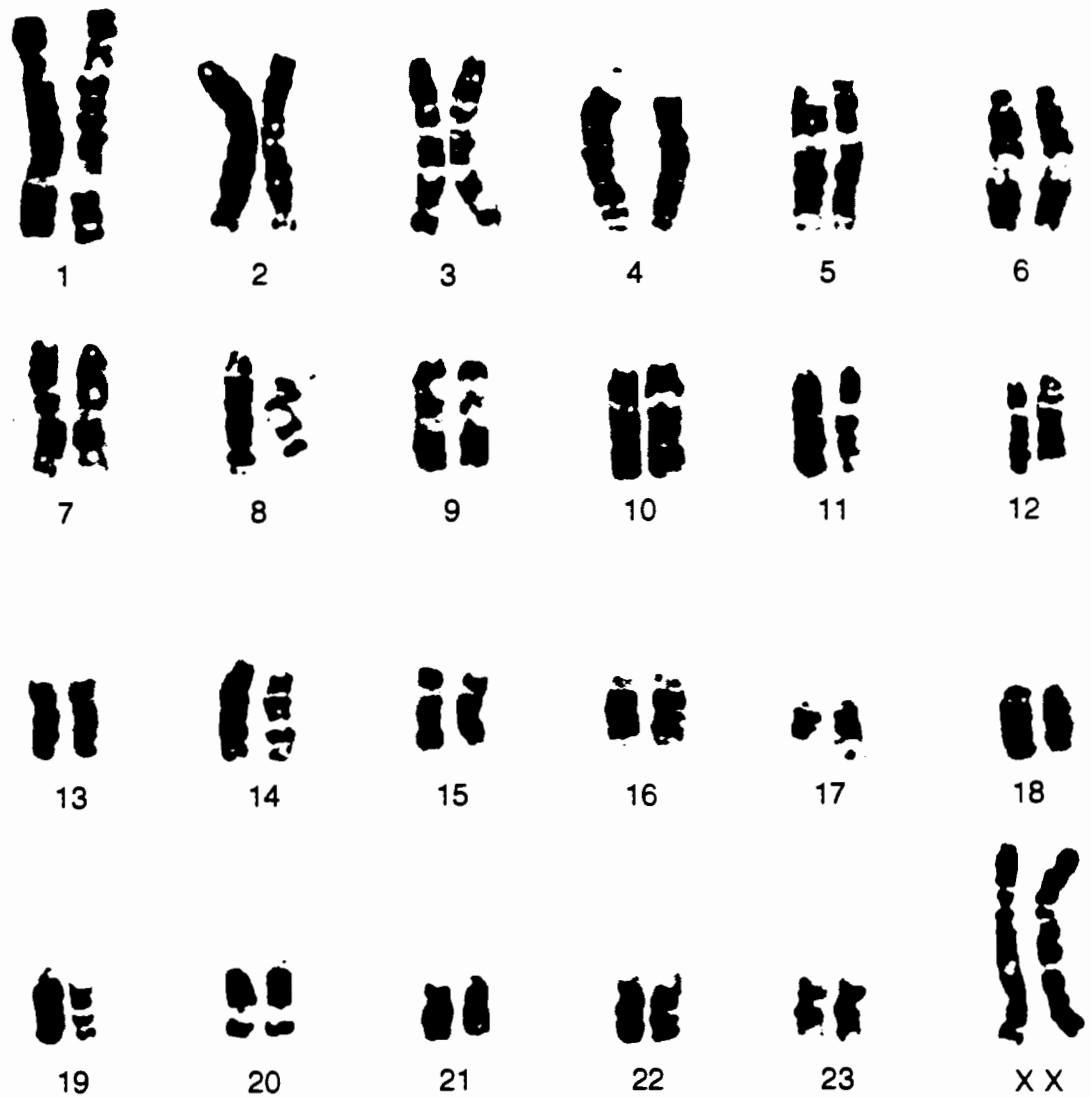


Fig. 2. G-banded karyotype of a female *Peromyscus boylii* (FN = 52).

Nomenclature of the chromosome bands

The report of the 1977 Committee for the Standardization of Chromosomes of *Peromyscus* suggested that the methods of the human chromosome nomenclature (ISCN) be used in describing the chromosome conditions in *Peromyscus*. To the extent possible, we have followed these conventions in developing the chromosome band nomenclature for *Peromyscus*. However, differences between the karyotypes of *Homo sapiens* and *Peromyscus*, and between a system tailored for a single species as opposed to one applicable for many species (entailing a substantial number of "normal" chromosome arrangements) have necessitated various departures from the methods of the ISCN. Where necessary, the chromosome band nomenclature presented here is based on the methods of chromosome nomenclature for laboratory mice (Committee on Standardized Genetic Nomenclature for Mice, 1972).

Table II. Comparison of chromosome numbers in the original (1977) standardized *Peromyscus* karyotype and the revised karyotype presented in Fig. 1

1977 Ideogram	Revised Ideogram
1-7	no change
8	rotated 180°
9	no change
10	equals 12
11	equals 10
12	equals 13
13	equals 11
14-16	no change
17	equals 18
18	equals 17
19-23	no change

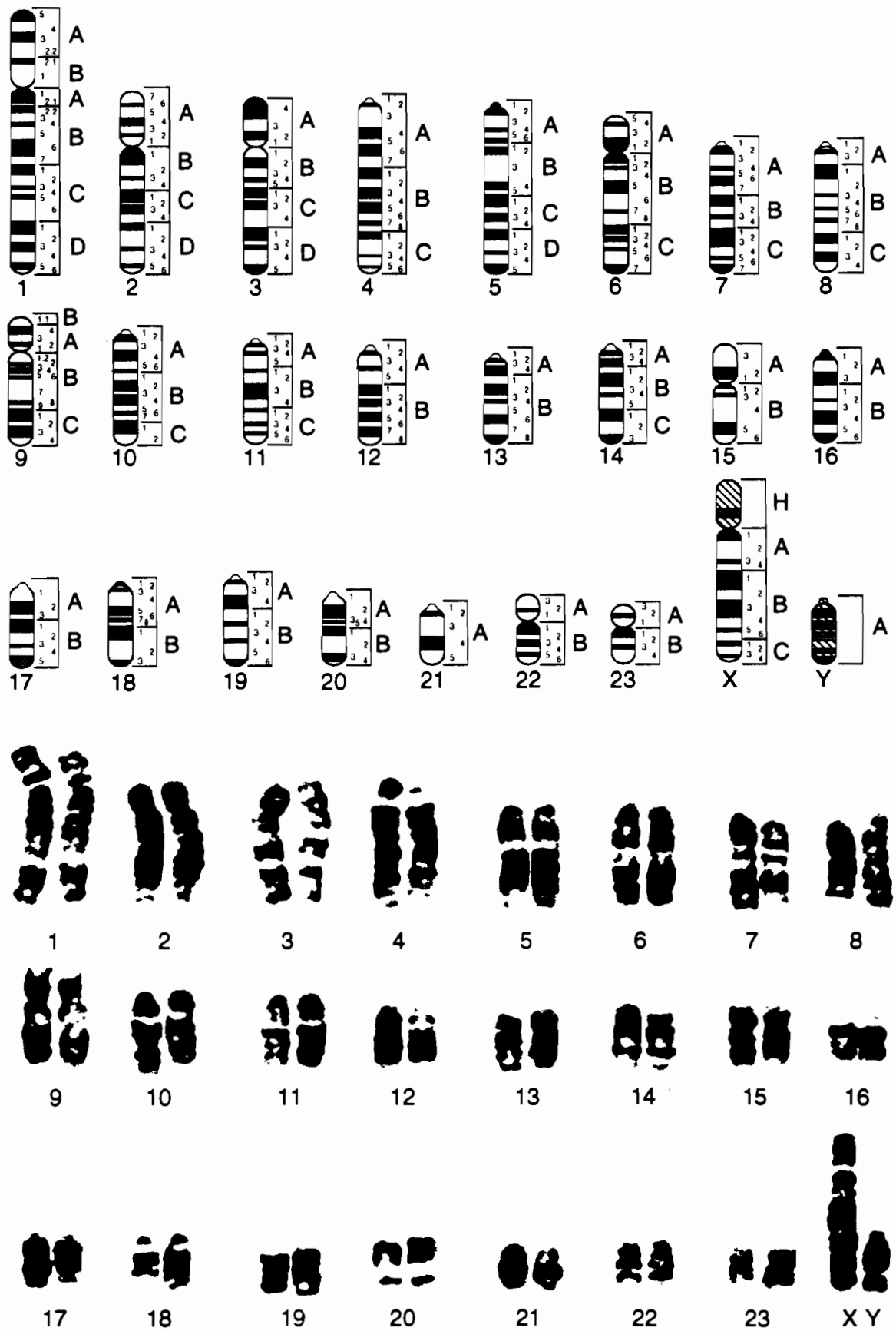


Fig. 3. Ideogram (top) and G-banded karyotype (bottom) of a male *Peromyscus truei* (FN = 62).

For a subset of the G-banded karyotypes compared, equally enlarged micrographs were analyzed mensurally. Measurements of the relative position and band widths for 70 G-banded karyotypes (representing 12 species) were used as the basis for the bands presented in the revised ideogram (Fig. 1). The revised FN = 52 ideogram was originally generated by hand and then transferred to a Macintosh computer using the program Canvas version 3.03 (Deneba Systems, Inc.). The computer-based ideogram allows future revisions to be readily incorporated and makes it relatively easy to construct ideograms for different deer-mouse karyotypes whether they represent species, subspecies, populations or even individuals (see Figs. 3 and 4). Construction (from the FN = 52 ideogram) of ideograms for alternative karyotypes does not disturb the nomenclature of the chromosomes or their chromosomal bands. Computerized versions of the ideogram also have the advantage of being readily and accurately transferred among investigators. Copies of the computer files for the ideograms presented here are available from the principal author.

As in other chromosomal standardizations, a band was defined as a part of a chromosome which is distinguishable by virtue of its lighter or darker staining intensity. The ideogram for the 1977 standardized karyotype used black to designate "major" and gray to indicate "minor" bands. However, the definitions of major and minor bands were not specified. In this revision we use black to denote those dark G-bands which appear consistently (major bands) and gray (stippled) for dark G-bands which variably appear (minor bands). White bands represent lightly or negatively stained regions in G-banded metaphases.

Whereas the 1977 standardization of the chromosomes of *Peromyscus* depicted 211 autosomal bands, the revised FN = 52 ideogram describes a total of 318 bands. The FN = 52 condition of *Peromyscus boylii* was used as the reference for establishing the G-band nomenclature. For each chromosome, the G-bands are grouped into regions which are designated alphabetically. Within these regions, bands are sequentially numbered distal to the centromere. We follow the ISCN in using a decimal point to denote subdivision within a band (e.g., Figs. 4 and 5). Regions of noncentromeric C-band positive heterochromatin have been designated with an "H" and indicated by cross hatching. Interstitial heterochromatic additions should be labeled as an "H" band within the appropriate alphabetic region.

The euchromatic arm of the X chromosome and its G-band pattern are conserved among the species of *Peromyscus*. We treat the euchromatic arm of the X chromosome in the same manner as euchromatic portions of the autosomes. In most species of *Peromyscus*, a heterochromatic arm is present on the X chromosome. As with autosomal heterochromatin, we designate this region with an "H." Varied G-band patterns are sometimes visible in the heterochromatic arm of the X chromosome of *Peromyscus*. Lacking information on the interspecific homology of the heterochromatin of the X chromosome, we indicate (on the ideograms) bands within this region as minor bands but do not give them numerical designations.

The Y chromosome of *Peromyscus* typically displays little, if any, distinct G-banding. In well-banded metaphases, the Y

chromosome is often identified as the unbanded element. The Y chromosome generally has been described as entirely heterochromatic (C-band positive) although some reports note differences in C-band intensities within the Y or small portions of the Y which seem to be C-band negative. For biarmed conditions of the Y chromosome, we designate one arm as region A and the other as region B. We recommend that, where appropriate data are available, the pseudoautosomal portion of the Y chromosome (Hale, 1992) be used to designate the A region. As in the case of the G-bands in the heterochromatic arm of the X chromosome, we do not numerically designate the inconsistently appearing G-bands of the Y chromosome.

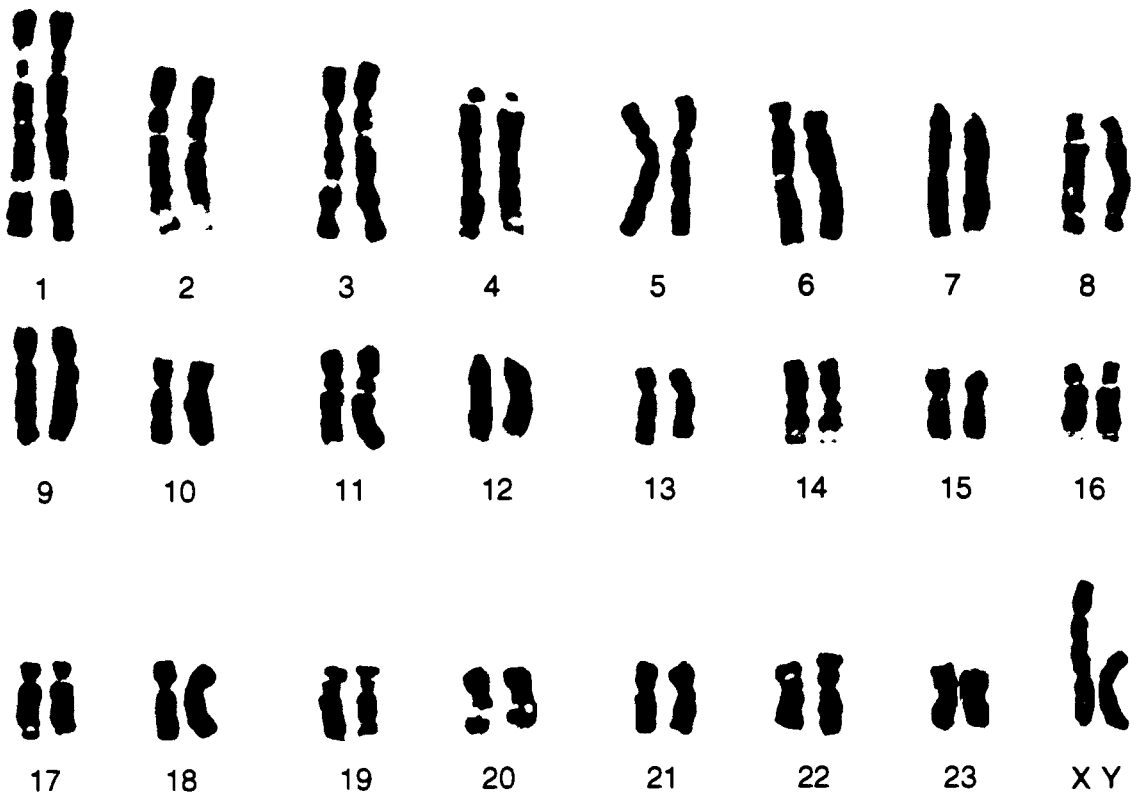
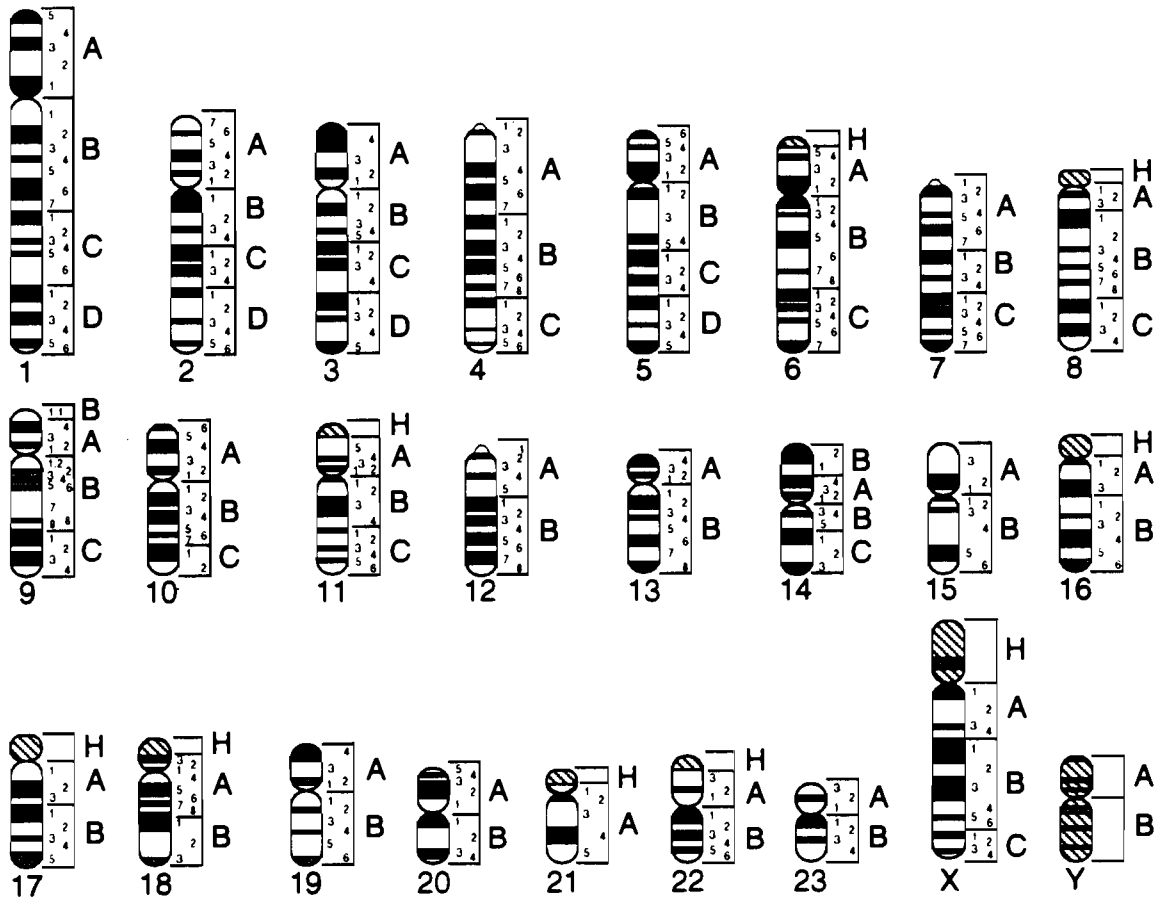
The revised ideogram – euchromatic karyotype

The majority of the autosomes of *Peromyscus* have distinctive G-bands or sets of G-bands which enable their reliable identification. Chromosomal identifications and analyses of karyotypic differentiation and variation are, however, occasionally complicated by the presence of noncentromeric heterochromatic regions (see below). The following discussion presents a description of the euchromatic complement of the autosomes and X chromosome of *Peromyscus*. In this discussion, we identify the specific G-bands or intrachromosomal G-band patterns which are most frequently useful in identifying each of the chromosomes of *Peromyscus*. Although we provide general comparisons of chromosome size, we note that differential contraction causes considerable variation in the lengths of metaphase chromosomes, sometimes even effecting the apparent lengths of homologs within individual cells. We catalog the more problematic identifications and indicate the likely chromosome misidentifications. For each chromosome, we also present an overview of the previously reported euchromatic rearrangements; citations for these data are presented in Table I. We emphasize, however, that because most of the G-band studies of *Peromyscus* examined only a small number of individuals, the available data undoubtedly underestimate the extent of intraspecific chromosome variation.

Chromosome 1. Chromosome 1 is typically the largest of the chromosomes in *Peromyscus*. This chromosome may be rivaled in size by the other large chromosomes (2, 3 and the X) when these have substantial heterochromatic short arms. Chromosome 1 usually G-bands well with the minor bands being fully distinguishable in more elongate preparations. The overall G-banded pattern of Chr 1 is readily recognizable. The light staining of the relatively large region 1C2 to 1C6 and the three distinctive major bands at the distal (noncentromeric) end of the chromosome (1D1, 1D3, 1D5) are typically diagnostic.

Within the genus *Peromyscus*, Chr 1 is most frequently biarmed with the morphology characteristic of the FN = 52 condition shown in Figs. 1 and 2. *P. truei* is characterized by an alternate biarmed condition (Fig. 3) which apparently resulted from an interstitial pericentric inversion as diagrammed in Fig. 5. In *P. beatae*, polymorphism of Chr 1 involves an acrocentric condition and both biarmed conditions.

Chromosome 2. Chromosome 2 is typically about three-fourths as large as Chr 1 and is similar in size to Chr 3, 4 and



sometimes the X. Chromosome 2, however, is not easily confused with any of these chromosomes and is usually recognizable by the relative absence of major G-bands at the distal end of the chromosome (region 2D2 to 2D6). While Chr 4 also has a lightly stained distal region, the rest of the G-banding pattern of Chr 2 is unlike that of Chr 4.

Relatively few species of *Peromyscus* possess an acrocentric condition of Chr 2 (Figs. 1 and 2). Most species display the biarmed condition in which the centromere is located between bands 2A1 and 2B1 (Figs. 3 and 4). In *P. leucopus*, band 2D5 is a major band which appears to correspond to an interstitial C-band; this condition is characteristic of and apparently diagnostic for this species.

Chromosome 3. Typically similar in size to Chr 2 and some X chromosomes, the most distinctive feature of Chr 3 is the pattern formed by bands 3B2, 3C1, 3C3, and 3D1. In less elongate preparations, bands 3C1 and 3C3 may appear as a single band. The overall G-band patterns readily distinguish Chr 3 from Chrs 2 and 4. Compared to the euchromatic portion of the X chromosome, Chr 3 is distinguished by the narrower width and closer positioning of bands 3C1 and 3C3 as compared to XB1 and XB3.

About one-third of the species examined to date display the acrocentric condition of Chr 3 (Figs. 1 and 2) or have a heterochromatic short arm attached to this condition. The remainder possess the biarmed condition in which the centromere is located between bands 3A1 and 3B1 (Figs. 3 and 4).

Chromosome 4. Although frequently similar in size to the euchromatic portions of Chrs 3 and 5, Chr 4 is one of the most easily identified chromosomes of *Peromyscus*. Band 4A3 provides a distinctive nonstaining area proximal to the centromere and the sequence of major bands from 4A4 to 4C1 is unique. Bands 4C3 and 4C5 do not stain with the intensity of the more proximal major bands and consequently, the distal portion of Chr 4 (4C4 through 4C6) is typically lightly stained.

Chr 4 is one of four autosomes of *Peromyscus* for which there has been no report of euchromatic rearrangements.

Chromosome 5. The euchromatic Chr 5 is generally similar in size to Chr 4 but may appear similar in size to Chr 6–8. Chromosome 5 is most easily recognized by the nonstaining region 5B3 and the distal dark region comprised of bands 5B4 to 5D1. Compared to Chr 6, the nonstaining region 5B3 is smaller and more proximal to the centromere than is the lightly-staining region constituted by bands 6B6 to 6B8. Although Chr 5 may superficially resemble Chr 2, the euchromatic portion of Chr 5 is noticeably shorter than the comparable section of Chr 2.

About two-thirds of the species examined display the acrocentric condition of the euchromatic portion of Chr 5. Apparently identical biarmed conditions of Chr 5, resulting from independent but cytologically indistinguishable pericentric inversions, have arisen at least three times within the genus (Rogers et al., 1984; Stangl and Baker, 1984; Smith, 1990). Biarmed

Fig. 4. Ideogram (top) and G-banded karyotype (bottom) of a male *Peromyscus maniculatus* (FN = 86). The ideogrammatic representation of Chr 9 exemplifies the use of a decimal for indicating subdivision (rearrangement) within the bands of the FN = 52 standardized karyotype (see also Fig. 5).

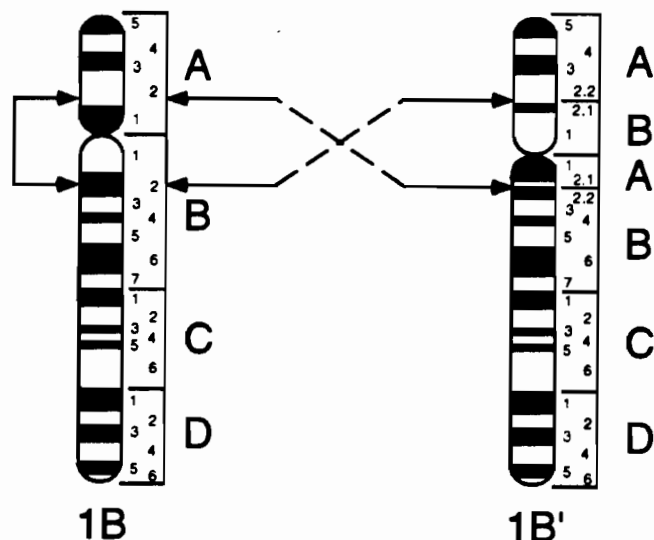


Fig. 5. Ideogrammatic representation of the presumed primitive (1B) and derived (1B') conditions of Chr 1. The ideogram for the 1B' condition exemplifies the use of a decimal for indicating subdivision within the bands of the FN = 52 standardized karyotype.

and acrocentric conditions of Chr 5 distinguish the two cytotypes of *P. leucopus*.

Chromosome 6. Generally similar in size to Chrs 5 through 8, the euchromatin of Chr 6 is most easily distinguished by the lightly-staining region constituted by bands 6B6 to 6B8. In addition to the differences from Chr 5 as described above, the bands 6C1 to 6C6 generally give Chr 6 a distinctive and darkly stained distal region.

Some variability occurs in the position of band 6B5 within *P. maniculatus*. In some populations, the presence or absence and position of an interstitial C-band in the 6B region causes a slight proximal or distal shift in the position of band 6B5 (compare Chr 6 in Figs. 2 and 3 of Gunn, 1988).

Chromosome 6 has experienced at least seven independent pericentric inversions (Rogers et al., 1984; Stangl and Baker, 1984) and among species, Chr 6 is as likely to be biarmed as acrocentric. There are at least three morphologically different biarmed forms of the euchromatic constitution of Chr 6 (Stangl and Baker, 1984). *Peromyscus maniculatus*, *P. oreas*, *P. sitkensis*, and *P. levipus* have been reported to display pericentric inversion polymorphisms of Chr 6. The inversion polymorphism for Chr 6 in *P. maniculatus* includes the acrocentric and two different biarmed conditions (Greenbaum and Reed, 1984; Hale, 1989).

Chromosome 7. The euchromatic Chr 7 is also about the same size as the comparable portions of Chr 5–8. Chromosome 7 is usually distinguished by the major band near the centromere (7A2) and by the distinctive dark region constituted by bands 7C1 and 7C3. The latter bands frequently appear as a single large dark band. This dark region is more distant from the distal telomere than is a similar region (9C1 to 9C3) in Chr 9.

About three-fourths of the species examined display the acrocentric condition of Chr 7. However, two different

biarmed conditions of Chr 7 have been reported (Smith, 1990) and polymorphism for the acrocentric and a biarmed condition (with the centromere adjacent to band 7B1) occurs in *P. maniculatus*, *P. oreas* and *P. sitkensis*.

Chromosome 8. Similar in size to Chr 7–9, the euchromatic portion of Chr 8 is typically distinguished by the dark bands 8B1, 8C1 and 8C3. Compared to markers of Chr 7, band 8B1 is farther from the centromere than is 7A2 and bands 8C1 and 8C3 are farther apart and typically more distinct than are bands 7C1 and 7C3. Compared to Chr 9, bands 8C1 and 8C3 are smaller and farther apart than are bands 9C1 and 9C3 (i.e., band 8C2 is wider than band 9C2).

There has been no report of euchromatic rearrangement of Chr 8.

Chromosome 9. Although overtly similar to both Chr 7 and 8, Chr 9 is one of the most readily recognizable chromosomes of *Peromyscus*. Chromosome 9 is distinguished by the large major bands 9C1 and 9C3 near the distal end of this chromosome. A small G-negative band (9C4) is typically present at the distal telomere. Chromosome 9 is also characterized by the relatively large and lightly-staining regions comprised by 9A4 to 9B3 and 9B5 to 9C1. In biarmed conditions of Chr 9, the more proximal of these regions (9A4 to 9B3) becomes split with a portion occupying the distal region of the short arm (Figs. 3 and 4).

Acrocentric conditions of the euchromatic portion of Chr 9 occur in species which have a predominance of acrocentric chromosomes (relatively low fundamental number). Most of the species for which banding data are available have biarmed conditions of Chr 9.

Chromosome 10. Chromosome 10 is in the same euchromatic size range as Chrs 11 and 12, however, it is the only element of this size to have five major G-bands. Chromosome 10 is most easily recognized when acrocentric. In species with higher fundamental numbers, the biarmed condition of Chr 10 can be difficult to distinguish from a variety of other medium-sized chromosomes.

Most species of *Peromyscus* display the acrocentric condition of Chr 10. Biarmed conditions of this chromosome have been reported in some members of the *boylii* and *maniculatus* species groups and in *Peromyscus* (= *Habromys*) *lepturus*.

Chromosome 11. Chromosome 11 is most readily distinguished by the prominent dark band 11B3 and the immediately proximal and distinctive nonstaining region 11B2. The other bands in this chromosome are not consistently distinguishable.

About two-thirds of the species for which G-bands have been described display the acrocentric condition of the euchromatic portion of Chr 11. Two different biarmed conditions have been described for this chromosome (see Smith, 1990). Biarmed and acrocentric conditions of Chr 11 distinguish the two cytotypes of *P. leucopus*.

Chromosome 12. Among the chromosomes in this size range, Chr 12 is distinguished by the large dark area constituted by bands 12B1 to 12B7. The G-negative band 12B8 is characteristic of the distal telomere.

To date, only one species (*P. melanotis*) has been reported to display a biarmed condition of the euchromatic portion of Chr 12.

Chromosome 13. The euchromatic compositions of Chr 13–20 may all be of similar size and this group includes most of the more difficult-to-identify chromosomes of *Peromyscus*. Chromosome 13 in particular has no prominent or distinguishing G-band features and generally does not band well. When band 14C3 is absent or weakly expressed, the distal band 13B8 may be used to identify Chr 13.

Little euchromatic variation has been reported for Chr 13. Of the species for which data are available, a biarmed condition of the euchromatic portion of Chr 13 occurs in *P. maniculatus* and has been reported as a polymorphism in *P. aztecus* and *P. spicilegus*.

Chromosome 14. Among the intermediate-sized chromosomes of *Peromyscus*, Chr 14 is distinguished by the pattern established by major bands 14A4, 14B2 and 14C1. The G-negative bands 14B5 and 14C2 usually cause band 14C1 to be prominent and diagnostic. Band 14C1 is usually more distinct than are similarly positioned bands in Chr 15 and 16. Additionally, band 15B5 is closer to the distal telomere than is 14C1.

Most species display the acrocentric condition of the euchromatic Chr 14 but biarmed conditions characterize most of the species in the *maniculatus* group and *P. spicilegus*. A pericentric-inversion polymorphism of Chr 14 occurs in some populations of *P. maniculatus* (Gunn, 1988).

Chromosome 15. The euchromatic Chr 15 is typically distinguished by bands 15A2 (adjacent to the centromere) and 15B5 near the distal end of the chromosome. The other bands in this chromosome are frequently unresolved.

A few species display the biarmed condition of the euchromatic portion of Chr 15 and two species, *P. maniculatus* and *P. aztecus*, harbor pericentric-inversion polymorphisms.

Chromosome 16. The most distinguishing feature of Chr 16 is the intense G-positive band 16A3. This band occurs as a relatively wide and single dark band in the proximal portion of Chr 16. The light bands 16B1 and 16B3 are frequently poorly expressed so that the entire region from 16A3 to 16B4 can appear darkly stained. Band 16B4 is usually less discrete than those in similar regions of Chr 14 and 15.

The acrocentric condition of the euchromatic portion of Chr 16 occurs in all deer-mouse species for which chromosome banding data are available. A biarmed condition of Chr 16, resulting from a pericentric inversion and with the centromere located between 16A1 and 16B1, has been reported for a population of *P. maniculatus* from Kansas (McAllister, 1992).

Chromosome 17. In most species of *Peromyscus*, there is little difference in size among Chr 17–23. Chromosome 17 is typically distinguished by the G-negative staining of the centromere and the proximally-positioned dark region resulting from bands 17A2 and 17B1. These latter two bands may be distinct or appear as a single large dark region. Most species also display the minor dark band 17B5 at the distal telomere.

There have been no reports of rearrangement of the euchromatic acrocentric Chr 17 in *Peromyscus*.

Chromosome 18. Chromosome 18 is most readily recognized by bands 18A3, 18A5 and 18B1. Bands 18A5 and 18B1 are close together and frequently appear as a single large dark region.

Biarmed conditions of the euchromatic component of Chr 18 have been reported only for *P. maniculatus* and *P. leucopus*. Although these two biarmed conditions do not appear identical, band 18A3 provides a distinctive marker in the short arm in both cases.

Chromosome 19. Chromosome 19 is difficult to differentiate (particularly in more contracted preparations) and is consequently among the most frequently misidentified chromosomes of *Peromyscus*. Chromosome 19 frequently bands poorly and the total number of possible G-bands is rarely expressed. When acrocentric, Chr 19 can appear quite similar to Chr 17 and 18. The size of the region from 17A2 to 17B1 will generally distinguish Chr 17 from 19 and the negatively-stained region 18B2 will usually distinguish Chr 18 from 19. When biarmed, Chr 19 can be nearly identical to Chr 22. This is particularly true if there is telomeric heterochromatin present on the short arm of 22 (compare these chromosomes in Fig. 4). Sequential G- and C-banding is recommended to differentiate Chr 19 in forms where it is biarmed.

Biarmed conditions of the euchromatic component of Chr 19 are known only for *P. polionotus*, *P. oreas* and *P. sitkensis*.

Chromosome 20. Chromosome 20 is another of the most readily recognized autosomes of *Peromyscus*. The diagnostic feature is the distinct G-negative region 20B2, a region usually clearly differentiated by the dark staining major bands 20A2 and 20B1 proximally and 20B3 distally. The distinction of 20B2 is retained whether the chromosome is acrocentric (Figs. 2 and 3) or biarmed (Fig. 4).

The euchromatin of Chr 20 is acrocentric in most species of *Peromyscus*. Biarmed conditions appear to characterize species in the *maniculatus* group and *P. spicilegus*. Alternative acrocentric and biarmed conditions of Chr 20 distinguish the two cytotypes of *P. leucopus*.

Chromosome 21. When a C-band positive short arm is not present, Chr 21 is typically smaller than Chr 18–20. In most G-band preparations, Chr 21 exhibits only one prominent major band, 21A4.

The euchromatin of Chr 21 has been reported as uniformly acrocentric in *Peromyscus*. However, sequential G- and C-banding of more elongate preparations has indicated a small pericentric inversion of Chr 21 in *P. maniculatus luteus* (Fig. 4). The extent to which this condition characterizes *P. maniculatus* is yet to be determined.

Chromosome 22. Chromosome 22 is usually biarmed, larger than Chr 23 and has a greater number of major bands in the "B" region. Chromosome 22 is also more likely to have heterochromatin present at the distal end of the short arm. As noted above, this can cause Chr 22 to have a G-banding pattern nearly identical to that of Chr 19. Chromosome 22 can usually be differentiated from Chr 19 by the distal non-staining region 22B6.

The acrocentric condition of the euchromatic Chr 22 has been reported only as a polymorphism within *P. beatae*.

Chromosome 23. Chromosome 23 is typically the smallest of the autosomes of *Peromyscus*. This chromosome usually has a dark G-band at the centromere (23B1) and single dark bands in each arm. Chromosome 23, however, generally G-bands poorly and other than staining at 23B1 this chromosome may stain homogeneously.

The acrocentric condition of the euchromatic Chr 23 has been reported only for *P.* (= *Isthmomys*) *pirrensis* and as a polymorphism within *P. beatae*.

X Chromosome. The euchromatic constitution of Chr X has two very distinctive major bands, XB1 and XB3. These bands are typically wider and farther apart than are similar bands (3C1 and 3C3) on Chr 3. Although the euchromatic portion of Chr X approximates the euchromatic size of Chr 6, Chr X usually possesses a heterochromatic short arm and the entire Chr X is frequently similar in size to Chr 2 and 3. The extent of the heterochromatic short arm of Chr X differs among species and has been documented to vary within species and between homologs within individual females (Sudman and Greenbaum, 1990).

The euchromatic component of Chr X appears uniformly stable among species of *Peromyscus*. An apparent inversion altering the G-band pattern in the X chromosome in one of 118 individuals of *P. leucopus* (Baker et al., 1983) is the only report of variation involving the euchromatic portion of Chr X in *Peromyscus*.

Autosomal heterochromatin

There is extensive interspecific differentiation and intraspecific variation for C-band positive heterochromatin in *Peromyscus* and its close relatives. The presence and location of such noncentromeric heterochromatin can complicate identification of individual chromosomes and should be considered in any analysis of the chromosomes of peromyscine rodents. Most of the chromosomal research on *Peromyscus* has inferred the location of heterochromatin by arranging C-banded karyotypes to correspond with G-banded karyotypes of the same individuals. This method has undoubtedly resulted in some inaccurate descriptions. This problem can be avoided by C-banding previously G-banded chromosomes and this technique is recommended for taxa in which the location of heterochromatin is not obvious. The C-band positive locations in Fig. 4 were determined in this manner.

Chromosome 1 is the only chromosome of *Peromyscus* which has not been reported to have some occurrence of a heterochromatic short arm or heterochromatin associated with the distal portion of an otherwise euchromatic short arm. Although the short arm of Chr 1 sometimes C-bands more darkly than is typical for euchromatin, early reports (Pathak et al., 1973; Arrighi et al., 1976) that the short arm of Chr 1 is heterochromatic have not been supported by subsequent studies.

Among deer mice, the presence of short-arm heterochromatin generally conforms to three patterns. A few species, such as *P. eremicus*, *P. merriami* and to a lesser extent *P.* (= *Isthmomys*) *pirrensis*, have whole-arm heterochromatin added to an otherwise mostly acrocentric karyotype. Species in the *leucopus* and *maniculatus* groups exhibit short-arm heterochromatin on a variety of chromosomes and are frequently polymorphic for the presence and absence of this heterochromatin. The presence of telomeric heterochromatin on otherwise euchromatic short arms has been reported for *P. maniculatus* (Fig. 4) and *P. leucopus* (Robbins and Baker, 1981). Intraspecific polymor-

phism for the presence of such telomeric heterochromatin has been observed in *P. maniculatus* (McAllister, 1992).

Compared to the variation in whole-arm or short-arm telomeric heterochromatin in *Peromyscus*, variation for the presence of interstitial heterochromatin is less common. Several authors (Arrighi et al., 1976; Robbins and Baker, 1981; Baker et al., 1983) have reported the presence of inconsistent interstitial C-bands in Chr 1, 4 and 7 in *P. leucopus*. The karyotype of *P. leucopus* also appears to be characterized by a unique and consistent interstitial C-band near the distal end of the long arm of Chr 2 (Robbins and Baker, 1981). This unique band of interstitial heterochromatin appears to constitute the G-band 2D5 in this species. Interstitial C-bands have also been reported for Chr 5, 6, and 7 in northwestern populations of species in the *maniculatus* species group (Pengilly et al., 1983; Gunn and Greenbaum, 1986; Hale, 1986; Gunn, 1988). Although the position of the interstitial C-band in Chr 6 alters the position of band 6B5 (see above), none of the aforementioned interstitial C-bands complicates the identification of involved chromosomes, and in some cases (see Hale, 1986) the interstitial C-bands can facilitate the use of these chromosomes in cytogenetic analyses. A relatively large block of interstitial heterochromatin which occurs in low frequency in *P. beatae*, however, required meiotic analysis for its identification on Chr 22 (Sudman et al., 1989).

Sex heterochromatin

There is substantial variation in the presence/absence and extent of heterochromatin associated with the sex chromosomes of *Peromyscus*. The length of the heterochromatic short arm of Chr X varies not only among species, but often within species and even between homologs within individual females (e.g., Sudman and Greenbaum, 1990). In size and conformation, Chr Y varies from being acrocentric and tiny (*P. perfulvus* and *P. megalops*) to being submetacentric and as large as Chr 4 (for review see Hale et al., 1991). In some species (e.g., *P. beatae*) Chr Y is variable in both size and conformation (Sudman and Greenbaum, 1990). Several lines of evidence suggest that the sex heterochromatin (noncentromeric heterochromatin of Chr X and Y) of deer mice constitutes a type of chromosomal material which is characteristically different from both euchromatin and autosomal heterochromatin. Baker and Wichman (1990) demonstrated a disproportionately high concentration of the retrotransposon *mys* in sex heterochromatin as compared to autosomal euchromatin of *Peromyscus*; *mys* elements were not present in the autosomal heterochromatin of *Peromyscus*. For ten species of *Peromyscus*, Hamilton et al. (1992) demonstrated that a single family of repeated elements hybridized to all centromeric and autosomal short arm heterochromatin. With the exception of three distinct bands in the short arm of Chr X in *P. eremicus*, however, this same probe did not hybridize to noncentromeric heterochromatin of the X or Y chromosome. Further, although Dominguez (1991) showed that the autosomal heterochromatin of *Peromyscus* is highly resistant to aphidicolin-induced breakage, McAllister (1992) documented the existence of an aphidicolin-induced fragile site

in the heterochromatic arm of Chr X in *P. maniculatus*. Meiotic studies (see below) indicate that the sex heterochromatin behaves differently than does autosomal heterochromatin. The sex heterochromatin of *Peromyscus* provides fertile ground for future research and needs to be considered as being subject to a unique subset of cytogenetic mechanisms and phenomena.

Meiotic behavior of the chromosomes of *Peromyscus*

Studies of meiosis have provided detailed knowledge concerning synapsis, recombination and segregation of the chromosomes of deer mice and have served to establish *Peromyscus* as a model for comparisons of meiosis in other mammals including humans. Data from *Peromyscus* (Greenbaum et al., 1986b) provided the first set of discrete criteria for identifying zygotene and pachytene substages in surface-spread preparations of the synaptonemal complex. Additionally, several studies (Greenbaum and Reed, 1984; Hale, 1986; Hale and Greenbaum, 1988b) document that in *Peromyscus* the inverted region of heterozygous pericentric inversions undergoes non-homologous synapsis (heterosynapsis) without the formation of an inversion loop. This process results in suppression of chiasmata in the inverted segments and normal segregation of the inverted chromosomes (Hale, 1986). There appears to be no basis for the assumption of underdominance associated with the segregation of chromosomes heterozygous for terminally positioned pericentric inversions in *Peromyscus*. This phenomenon, referred to as a form of "synaptic adaptation" has been hypothesized as a cellular mechanism accounting for karyotypic orthoselection for pericentric inversions in *Peromyscus* (Greenbaum et al., 1986a; Hale, 1986).

Homozygous regions of autosomal heterochromatin form segments of synaptonemal complex similar to those of euchromatic regions and apparently undergo typical synapsis (Greenbaum et al., 1986b; Hale, 1986). Autosomal heterochromatin does not, however, exhibit chiasmata at diakinesis nor does it appear to participate in recombination (Hale, 1986). Autosomal pairs heterozygous for heterochromatin have been shown to undergo synaptic adjustment and normal segregation (Hale and Greenbaum, 1988a; Sudman et al., 1989). Hale and Greenbaum (1988b) described the meiotic pairing for a *P. maniculatus* in which Chr 15 was heterozygous for a pericentric inversion and the presence of a heterochromatic short arm. Synapsis of this chromosomal pair involved direct heterosynapsis of the inverted region followed by synaptic adjustment of the heterochromatin heteromorphism.

Hale and Greenbaum (1986) provided a detailed description of the synapsis of the sex chromosomes of *P. sitkensis*. This and studies of other deer mice (Sudman and Greenbaum, 1989; 1990; Hale et al., 1991) documented that the sex heterochromatin of *Peromyscus* synapses and that a single chiasma is regularly formed within the synapsed heterochromatin. Unequal crossing over within the synapsed sex heterochromatin accounts for the variability in size of the sex chromosomes in *P. beatae* (Sudman and Greenbaum, 1990).

Intergeneric considerations and cytosystematics

The generic boundary of *Peromyscus* is a complex systematic problem which has been thoroughly reviewed by Carleton (1989). This is of particular concern as a major portion of the problem involves a lack of congruence between morphologic and karyotypic-based interpretations of evolutionary relationships among mice which have been considered as *Peromyscus* and other clearly allied species. Overall, most *Peromyscus* cytogeneticists are faced with choosing between the classifications recommended by Hooper (1968) and Carleton (1989). At the level of specific composition of the genus, the main question concerns the appropriate status of five taxa (*Podomys*, *Habromys*, *Osgoodomys*, *Megadontomys* and *Isthmomys*) which conventionally have been considered as subgenera of *Peromyscus* (see Hooper, 1968). Although Carleton (1980, 1989) recognized these taxa as genera, the mice in each of these taxa share the same set of chromosomes which characterize all of the species Carleton retains within *Peromyscus*. Accordingly, the chromosomal data are more consistent with Hooper's (1968) concept of *Peromyscus*. Data from in situ hybridization of satellite DNA (Hamilton et al., 1992) provide additional support for Hooper's circumscription of *Peromyscus*. Although not traditionally considered as congeneric with *Peromyscus*, mice in the taxon *Neotomodon* also have the chromosomal complement of *Peromyscus*. Cladistic analysis of the banded chromosomes of *Neotomodon* placed these mice well within indisputable taxa of *Peromyscus*. Based on these findings, Yates et al. (1979) recommended that *Neotomodon* be considered as congeneric with *Peromyscus*. Regardless of the details of the generic taxonomy, the standardized karyotype for *Peromyscus* applies directly to all of these species and the karyotypic data suggest that all of these mice constitute a common chromosome lineage.

In addition to its relevance for analyses among and within taxa in either concept of the genus *Peromyscus*, the 1977 standardized karyotype has proven useful for comparisons of the chromosomes of mice in a variety of other genera. Although the extent of chromosomal conservation decreases as comparisons involve taxa increasingly distant from *Peromyscus*, the 1977 standardized karyotype has been used to infer chromosomal homology in rodents as phylogenetically distant as the Old World murid genera *Rattus*, *Apodemus* and *Melomys* (Koop et al., 1984).

Among other taxa which have been considered within the tribe Peromyscini, *Onychomys* (grasshopper mice) and *Baiomys* (pygmy mice) display chromosomes most consistent with those of *Peromyscus*. Both *Onychomys* and *Baiomys* have diploid numbers ($2n$) of 48 with all chromosomes directly comparable to those in *Peromyscus*. Beyond this, however, the karyotype of *Onychomys* is more similar to that of *Peromyscus* than is that of *Baiomys*. The hypothesized primitive karyotype for *Onychomys* (Baker and Barnett, 1981) differs from the FN = 52 condition of *Peromyscus* by having biarmed (pericentric inverted) conditions of Chr 9 and 19. Differences in FN among grasshopper mice is due to the presence/absence of heterochromatic short arms (Baker et al., 1979; Baker and Barnett, 1981). *Baiomys taylori* possesses a karyotype with FN = 46, all autosomes being acrocentric (Yates et al., 1979), whereas *B. muscu-*

lus has FN = 65–66 with the variation and differences relative to *B. taylori* attributable to heterochromatic short arms (Robbins and Baker, 1981). These data support the karyotype of *B. taylori* as being primitive for a *Baiomys-Onychomys-Peromyscus* lineage with the biarmed conditions of Chr 22 and 23 representing a synapomorphy for *Onychomys* and *Peromyscus* (Engstrom and Bickham, 1983).

Morphology-based interpretations of the systematic relationship of *Nelsonia* (diminutive wood rat) are incompletely resolved and suggest that these mice represent an early offshoot of either the peromyscine lineage (Hooper and Musser, 1964) or its sister (neotomine) lineage (Carleton, 1980). G-banded chromosome data from a single individual of *Nelsonia* (Engstrom and Bickham, 1983), however, support its close association to *Peromyscus*. The entirely acrocentric karyotype of this specimen ($2n = 48$, FN = 46) was comprised of the same chromosome elements that characterize *Baiomys*, *Onychomys* and *Peromyscus*. Except for questions concerning the precise composition and band homology within a portion of Chr 1 (see Engstrom and Bickham, 1983; Koop et al., 1984; Rogers and Heske, 1984), the G-banded karyotype of *Nelsonia* is identical to that of *Baiomys taylori*.

Although morphologic analyses (Hooper and Musser, 1964; Carleton, 1980) have been interpreted to suggest a cognate relationship between *Reithrodontomys* (harvest mice) and *Peromyscus*, this relationship is not supported by the chromosomal data (Robbins and Baker, 1980; Rogers, 1983; Hood et al., 1984; Carleton, 1989). Within *Reithrodontomys* there are two karyotypic groups, one with high diploid numbers (50–52) and mostly acrocentric chromosomes and a second with low diploid numbers (38–42) comprised of entirely biarmed chromosomes (Hood et al., 1984 and references therein). The G-banded chromosomes for *Reithrodontomys* with high diploid numbers are comparable to those of the FN = 52 karyotype in *Peromyscus*. For each of the 23 autosomes of *Peromyscus*, Robbins and Baker (1980) identified G-band homologous elements within the $2n = 50$ karyotype of *R. fulvescens*; they were unable, however, to identify homology or origin for the remaining chromosome pair. G- and C-banded data for *Reithrodontomys* with $2n = 52$ are entirely comparable to those from *R. fulvescens* except for an additional pair of chromosomes (Hood et al., 1984). Chromosome evolution within *Reithrodontomys* displays a striking departure from the relatively conservative pattern observed within the *Baiomys-Onychomys-Peromyscus* lineage. Rearrangement between the high- and low- $2n$ forms of *Reithrodontomys* has been so extensive that relatively few of the chromosomes of low- $2n$ species could be identified to homologous arms in high- $2n$ karyotypes (Robbins and Baker, 1980; Hood et al., 1984). Differentiation between the high- and low- $2n$ karyotypes clearly involves numerous euchromatic and heterochromatic events (Hood et al., 1984). For the low- $2n$ species of *Reithrodontomys*, the standardized karyotype of *Peromyscus* has little value.

Morphologically, *Scotinomys* (brown mice) have not been considered to be closely related to *Peromyscus* (Carleton, 1980), although Hooper and Musser (1964) included *Scotinomys* within their concept of the Peromyscini. Comparative analysis of the G-banding patterns of *Scotinomys* ($2n = 58$, FN

= 88) indicates only a moderate amount of homology relative to the karyotype of *Peromyscus* (Rogers and Heske, 1984). Of the 29 pairs of chromosomes in *Scotinomys*, only five autosomes and the Chr X are directly comparable to conditions in *Peromyscus*; two additional autosomes are homologous to portions of autosomes of *Peromyscus*. Except for two homologies to the karyotype of *Ochrotomys*, Rogers and Heske (1984) were unable to identify any other homologies between *Scotinomys* and peromyscine species.

Although *Ochrotomys* (golden mice) was once considered as a subgenus of *Peromyscus*, various investigators have recognized the distinctiveness of these mice, and more recent analyses have questioned their inclusion within the peromyscines (see discussion in Carleton, 1980). Analysis of the G-banded patterns of golden mice ($2n = 52$, FN = 72) revealed few G-band homologies with any peromyscine rodent (Engstrom and Bickham, 1982). Of the chromosomes of *Peromyscus*, only Chr 2 and 3 appear intact within the karyotype of *Ochrotomys*; portions of *Peromyscus* Chr 3 and 4 also appear to be present in golden mice. The remainder of the chromosomes of golden mice, including Chr X, are extensively rearranged relative to those of *Peromyscus*. Engstrom and Bickham (1982) concluded that the homologous elements shared between *Ochrotomys* and peromyscines are also shared with some species of *Neotoma* (Mascarello et al., 1974; Mascarello and Hsu, 1976) and hypothesized these conditions as primitive for the inclusive species.

To postulate the primitive karyotype for the Cricetidae, Koop et al. (1984) compared the G-band patterns of *Peromyscus* to species of more distantly related cricetid (*Neotoma* and *Oryzomys*) and murid (*Rattus*, *Melomys*, and *Apodemus*) rodents. While limiting their comparison to the 14 largest autosomes and the Chr X, these authors found sufficient consistencies to warrant the use of the standardized karyotype of *Peromyscus* as the reference in proposing homologies. With the exception of Chr 1, there was complete euchromatic homology between the compared autosomes of *Peromyscus* and *Neotoma*. For species of *Oryzomys* with karyotypes most similar to *Peromyscus*,

the degree of chromosome homology is less than between *Peromyscus* and *Neotoma*, but Koop et al. (1984) identified at least partial homology for the 14 largest chromosomes of *Peromyscus*. While there is far less identifiable homology to the karyotypes of *Apodemus*, *Rattus*, and *Melomys*, Koop et al. (1984) used these comparisons to hypothesize primitive chromosome conditions for cricetid rodents. The primitive condition of Chr 1 was proposed to be like that in *Neotoma*; the constitution of Chr 1 of *Peromyscus* was proposed to have involved addition (translocation) of euchromatic material (but see Rogers and Heske, 1984). The cricetid primitive conditions of Chr 2, 3, 4, 6, 7, 8, 9, 10, 11, and 12 were hypothesized to be acrocentric and identical to those in the primitive (FN = 52) condition of *Peromyscus*. Although the primitive conditions of Chr 5, 13, and 14 could not be critically determined, Koop et al. (1984) suggested that for the ancestor of *Peromyscus*, *Neotoma*, and *Oryzomys*, these chromosomes were also acrocentric and as present in the FN = 52 karyotype of *Peromyscus*.

When considering the number of species (over 560) and genera (100) within the Cricetidae, chromosome banding data are available for a relatively small representation. The extensive retention of chromosome homology between the karyotype of *Peromyscus* and that hypothesized as primitive for the family, however, insures that the standardized karyotype of *Peromyscus* will continue to be critical to future comparative cytogenetic studies of these rodents. Phylogenetic distance and extensive repatterning of chromosome elements among the species of some cricetid genera (e.g., *Reithrodontomys* and *Oryzomys*) will, however, ultimately limit the degree to which the nomenclature for the chromosomes of *Peromyscus* can be accurately and appropriately applied.

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