

Cladistical analysis of primitive G-band sequences for the karyotype of the ancestor of the Cricetidae complex of rodents

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Abstract

Homologous segments identified by G-banding sequences of chromosomes of *Peromyscus boylii*, *Neotoma micropus*, *Oryzomys capito*, (Family Cricetidae) *Rattus norvegicus*, *Melomys burtoni*, and *Apodemus sylvaticus* (Family Muridae) were used to hypothesize a chromosomal condition for the cricetid ancestor. A critical assumption in proposing the primitive G-banding sequences for a given chromosome is that if the outgroup and ingroup taxa have a specific sequence, then the ancestor of the ingroup taxa also had that same sequence. Using this methodology, (chromosome numbers refer to proposed homology to the standardized karyotype for *Peromyscus*), we propose that: (1) the primitive banding pattern of chromosome 1 was identical to that of *Neotoma*; (2) the primitive patterns of chromosomes 2, 3, 4, 6, 7, 8, 9, 10, 11, and 12 were acrocentric and identical to those proposed as primitive for *Peromyscus* (Robbins & Baker, 1981); (3) the primitive banding patterns of 5 and 13 were undetermined; (4) a major portion of the banding patterns of 14 and X were present in the ancestral karyotype. Only the largest 14 autosomes and X were examined because the smaller elements had insufficient G-band definition to ensure reasonable accuracy. The karyotype ancestral to that of *Peromyscus*, *Neotoma*, and *Oryzomys* may be as above and the banding patterns of 5, 13, and 14 were acrocentric and identical to those shown for *Peromyscus*, *Neotoma*, and *Oryzomys* (Fig. 1). In the primitive karyotype, heterochromatin (C-band material) was probably limited to the centromeric regions. If the primitive karyotype is as described above, then it is possible to determine the direction, type, and magnitude of chromosomal evolution evident in the various cricetid lineages. Based on the available data, radiation from the ancestral cytotype is characterized by a nonrandom distribution of types of chromosomal changes. Within many genera, more rearrangements occur in the 14 largest autosomal chromosomes of some congeneric species than distinguish the proposed primitive conditions for the genera *Peromyscus*, *Neotoma*, and *Oryzomys*. It would appear that the extensive morphological radiation from the primitive cricetid ancestor as indicated by the presence of over 100 surviving genera within the family, was not accompanied by extensive karyotypic changes. The magnitude of chromosomal variation that accompanies speciation in these genera appears to range from no detectable chromosomal evolution to a radical reorganization of the genome.

Introduction

The potential impact of identifying the primitive aspects of the karyotype of the cricetid rodents can be realized when one considers the number of species (over 560) and genera (100) that have radiated

within the Cricetidae. Such diversity of taxa provides an excellent opportunity to identify patterns of chromosomal evolution which can be used to test current cytogenetic theory, such as those described in Bengtsson (1980); Bickham and Baker (1979); Bush *et al.* (1977); Hedrick (1981); Lande (1979); Tem-

pleton (1980); Wilson *et al.* (1974, 1975, and 1977); and White (1978). Critical to understanding these patterns is an accurate assessment of the primitive conditions for various points in the evolutionary sequence. After determining the primitive condition, it is possible to document direction, type, and magnitude of chromosomal evolution in various lineages. When the information is placed in a cladistic framework, it becomes possible to propose synapomorphies and sister groups as well as to estimate the magnitude of convergence. Once synapomorphies and sister groups are known, a systematic arrangement of taxa can provide a viable hypothesis for the evolutionary history of the group.

This paper presents comparisons of G- and C-banding patterns of *Rattus norvegicus*, *Apodemus sylvaticus*, *Melomys burtoni*, *Neotoma micropus*, *Oryzomys capito*, and *Peromyscus boylii* in order to identify an ancestral karyotype for several branch points in cricetid evolution. We have made two critical assumptions. First, we have assumed that G-band sequences shared between taxa represent G-band segments present in the karyotype of the most recent common ancestor to these two taxa. The second concerns the accepted systematic arrangement of taxa proposed by Anderson (1967) and Wood (1955). Specifically, we have assumed that: (1) *Rattus*, *Melomys*, and *Apodemus* (Muridae) shared a common ancestor after separation from *Oryzomys*, *Neotoma*, and *Peromyscus* (Cricetidae) and can serve as a legitimate outgroup; (2) *Oryzomys*, *Neotoma*, and *Peromyscus* shared a common ancestor after separating from *Melomys*, *Apodemus*, and *Rattus*, and (3) *Neotoma* and *Peromyscus* (see Carleton, 1980) shared a common ancestor after separating from *Oryzomys* (of the South American Cricetids as shown by Carleton, 1980).

Material and methods

An analysis of chromosomal variation in eleven species of *Oryzomys* indicated that considerable G-band homology was shared between *Oryzomys capito* and the proposed primitive for *Peromyscus* (Baker *et al.*, 1983a) and we have used that species in our analysis. Additional G-band homologies were noted among *Peromyscus boylii*, *Neotoma*

micropus, *Rattus norvegicus*, *Apodemus sylvaticus*, and *Melomys burtoni*. Because of the extensive homology observed among these general and the availability of a standard chromosomal numbering system for *Peromyscus* (Committee for Standardization of Chromosomes of *Peromyscus*, 1977), we used this numbering system as a reference in proposing G-band homology among taxa.

To ensure that there were a sufficient number of bands for accurate identification of G-band sequences, only the 15 largest chromosomal pairs (the X plus 14 largest autosomes) were examined for each taxon. The 15 largest chromosomes represent over 60% of the total chromatin as measured by the sum of chromosome lengths (*Neotoma micropus* 72%, *Peromyscus boylii* 77%, *Oryzomys capito* 65%, *Apodemus sylvaticus* 67%, and *Rattus norvegicus* 63%)

Specimens of *Oryzomys capito* were collected from Suriname, Marowijne, Olea Marie. The ten other species of *Oryzomys* used in this study are described in detail in Baker *et al.* (1983a). Specimens of *Neotoma micropus* were collected from Texas, Garza Co., 3 mi E Southland and the specimens of *Apodemus sylvaticus* were collected from England, Avon Co., Frenchay. *Rattus norvegicus* came from a laboratory stock at Texas Tech University. The *Melomys burtoni* G-bands were taken from Baverstock *et al.* (1980). The *Peromyscus boylii* G-bands were from Robbins and Baker (1981). Standard bone marrow chromosomal preparations of *Oryzomys* and *Neotoma* were made in the field. The bone marrow fixative suspension was frozen in liquid nitrogen, and slides for G- and C-banding were prepared later at Texas Tech University as described in Baker *et al.* (1982). Bone marrow preparations of *Apodemus sylvaticus* and *Rattus norvegicus* were made in the laboratory. G-bands were produced by trypsin digestion and Giemsa staining (Seabright, 1971, as modified by Baker *et al.*, 1982). C-band procedures were described by Stefos and Arighi (1971). Skins and skulls of voucher specimens were deposited in the Carnegie Museum of Natural History and The Museum, Texas Tech University.

Results

A comparison of the G-banded karyotypes of *Neotoma micropus*, *Peromyscus boylii* (the karyo-

types of *N. micropus* and *P. boylii* have been proposed as primitive for their respective genera, Mascarello & Hsu, 1976, and Robbins & Baker, 1981). *Oryzomys capito*, *Rattus norvegicus*, *Apodemus sylvaticus*, and *Melomys burtoni* revealed many G-banded chromosomal sequences that appeared

homologous (Fig. 1, also see fig. 8 in Baverstock *et al.*, 1980). In Table 1, the chromosomal character states of the 14 largest chromosomes are designated as either identical to (I) or modified from (M) *Peromyscus boylii* G-banded chromosomes. The variation seen among the G-band sequences of *Pero-*



Fig. 1. A comparison of haploid G-banded chromosomes of *Neotoma micropus* (N), *Peromyscus boylii* (P) *Oryzomys macconnelli* (O), *Apodemus sylvaticus* (A) and *Rattus norvegicus* (R). Chromosomes are numbered according to the standardized chromosomal numbering system for *Peromyscus* (Committee for Standardization of chromosomes of *Peromyscus*, 1977). The extensive proposed homologies among the smaller chromosomes of *Neotoma micropus* to the *Peromyscus* standard are shown in the lower left box (unpaired chromosomes are from *Neotoma micropus*). The lower right box contains the smaller haploid chromosomes of *Oryzomys macconnelli* (O), *Apodemus sylvaticus* (A), and *Rattus norvegicus* (R).

Table 1. A summary of the chromosomal G-banded character states of the largest 15 pairs in *Peromyscus boylii*, *Neotoma micropus*, *Oryzomys macconnelli*, *Apodemus sylvaticus*, *Rattus norvegicus*, and *Melomys burtoni*. Chromosomes identical to that of the *Peromyscus* standard are designated by 'I'. Those modified from the *Peromyscus* standard are designated by 'M'. The various modifications are designated by a 'prime' designation.

<i>Peromyscus</i> Standard	<i>Neotoma</i> <i>micropus</i>	<i>Oryzomys</i> <i>macconnelli</i>	<i>Apodemus</i> <i>sylvaticus</i>	<i>Rattus</i> <i>norvegicus</i>	<i>Melomys</i> <i>burtoni</i>
1	M	M'	M''	M'''	M
2	I	I	M	M''	M'
3	M	I	I	I	I
4	I	M	I	I	I
5	I	M	?	?	?
6	I	M	?	M''	I
7	I	I	M	I	I
8	I	M	I	?	I
9	I	I	I	?	I
10	I	I	I	I	I
11	I	M	I	I	?
12	I	I	I	?	?
13	I	I	?	?	?
14	I	I	M	M'	?
X	M	M'	M''	M'''	M''''

Peromyscus boylii, *Neotoma micropus*, *Oryzomys capito*, *Rattus norvegicus*, *Apodemus sylvaticus*, and *Melomys burtoni* are briefly considered below.

Chromosomes 1 and 2

In chromosome 1 the major portion of the long arm appeared identical in all species, although the upper region immediately adjacent to the centromere and a short arm, if present, was variable. Chromosome 1 appeared identical in both *Melomys burtoni* (representing Muridae) and *Neotoma micropus* (representing Cricetidae), thus leading us to hypothesize that this form represents the ancestral condition for cricetids. In chromosome 1, additional euchromatic material was present in varying amounts in *Peromyscus boylii*, *Apodemus sylvaticus*, and *Rattus norvegicus* (banding sequences of the additional material in each was unique), whereas reduced amounts were observed in *Oryzomys capito*. These conditions are considered derived. Chromosome 2 was nearly identical in all species except *Rattus norvegicus*, where there has been some loss of euchromatin at both the centromeric and telomeric regions. The primitive condition was hypothesized to be similar to that of *Peromyscus boylii*, *Neotoma micropus*, and *Oryzomys capito*.

Chromosomes 3 and 4

Chromosome 3 was identical in all species except *Neotoma micropus*, in which a heterochromatic-short-arm polymorphism was evident (Mascarello & Warner, 1974). The ancestral condition is hypothesized to be like that of *Peromyscus boylii* and *Oryzomys capito*. Chromosome 4 was identical (and proposed as primitive for the cricetids) in all species except *Oryzomys capito*. It appears in *O. capito* that a large paracentric inversion or a centric shift occurred because the centromere is at opposite ends of the G-band sequence (Fig. 1).

Chromosomes 5 and 6

Chromosome 5 was the same in *Peromyscus boylii* and *Neotoma micropus*, and a major portion of this G-band sequence was present in *Oryzomys capito*. In *Oryzomys capito*, however, a major segment of chromosome 6 was terminally attached to the centromeric end of the G-band segments identified as originating in chromosome 5. We were unable to positively identify any portion of chromosome 5 in *Rattus norvegicus*, *Melomys burtoni*, or *Apodemus sylvaticus*. Therefore, for the Cricetidae ancestor, we cannot propose a primitive condition

for chromosome 5. Chromosome 6 was the same in *Peromyscus boylii*, *Neotoma micropus*, and *Melomys burtoni*. In *Rattus norvegicus* only the lower portion of chromosome 6 was located on the end of a larger unidentified euchromatic segment. We were unable to identify any portion of chromosome 6 in *Apodemus sylvaticus*. The primitive condition is proposed to be like that found in *Neotoma micropus* and *Peromyscus boylii*.

Chromosomes 7 and 8

Chromosome 7 was identical (and proposed as the primitive condition for the cricetids) in all species, except *Apodemus sylvaticus*. In *Apodemus sylvaticus* there was additional euchromatic material proximal to the centromere. Chromosome 8 was the same in *Peromyscus boylii*, *Neotoma micropus*, and *Apodemus sylvaticus*, and possibly *Melomys burtoni* but altered in *Oryzomys capito*. In *Rattus norvegicus* chromosome 8 could not be identified. The primitive condition of chromosome 8 for the Cricetidae ancestor is proposed to be as in *Peromyscus boylii* and *Neotoma micropus*.

Chromosomes 9 and 10

Chromosome 9 was identical in all taxa except *Rattus norvegicus*, in which it could not be identified. The primitive condition appears to be shared in *Oryzomys capito*, *Neotoma micropus*, and *Peromyscus boylii*. Chromosome 10 appeared to be identical in all species, therefore, it is presumed to have been the same in the cricetid ancestral karyotype.

Chromosomes 11 and 12

Chromosome 11 was identical in *Peromyscus boylii*, *Neotoma micropus*, *Apodemus sylvaticus*, and *Rattus norvegicus* but additional euchromatin was present in *Oryzomys capito*. We were unable to identify any part of chromosome 11 in *Melomys burtoni*. The primitive condition is proposed to be like that in *Peromyscus boylii* and *Neotoma micropus*. Chromosome 12 appeared to be the same in *Peromyscus boylii*, *Neotoma micropus*, *Apodemus sylvaticus*, *Oryzomys capito*, and *Melomys burtoni* and therefore, represents the primitive condition for cricetids. Chromosome 12 could not be identified in *Rattus norvegicus*.

Chromosomes 13, 14 and X

Chromosome 13 was found only in *Peromyscus boylii*, *Neotoma micropus*, and *Oryzomys capito*, and we therefore cannot propose a primitive condition for the Cricetidae ancestor. Chromosome 14 was the same in *Peromyscus boylii*, *Neotoma micropus*, and *Oryzomys capito* but in *Rattus norvegicus* and *Apodemus sylvaticus* it had been modified, although major segments were still identifiable. This suggests that a major portion of chromosome 14 represents the primitive condition for the *Peromyscus*, *Neotoma*, and *Oryzomys* group. The X chromosome was highly variable, although an extensive G-band sequence appeared to be conserved in all taxa leading us to agree with Stock *et al.*, (1973) that the conserved G-band sequence was also present in the common ancestor.

Constitutive heterochromatin (C-band material)

Within the species examined, constitutive heterochromatin was usually limited to the centromeric regions of the chromosomes. The only exception was the polymorphic heterochromatic short arm of chromosome 3 in *Neotoma micropus* (Mascarello & Warner, 1974). This suggests that the primitive karyotype of the ancestor of Cricetidae also had autosomal heterochromatin limited to the centric regions.

Discussion

The fact that G-banding sequences have been conserved in cricetid taxa was first noted by Mascarello *et al.* (1974a). It is remarkable that the G-banding patterns have been conserved in so many of the 14 largest autosomal pairs (Fig. 1). Although it is possible that an example or two of the proposed shared homology might represent convergent evolution (convergent chromosomal evolution has been documented in *Peromyscus*, Robbins & Baker, 1981), it is probable that most if not all of the identical G-banding sequences we have described as primitive are the result of conservation of banding sequences that were present in a common ancestor of the family Cricetidae. Although we used only 6 taxa in the above cladistic analysis, the sequences we have proposed as primitive are found in several cricetid genera (see next paragraph for citations).

Several other genera of murids could also be used equally as well as outgroups (Baverstock *et al.*, 1983).

Though the vast majority of taxa in the Muridae and Cricetidae remain to be G-banded, the available studies contribute to an understanding of G-band evolution. To assess the various chromosomal conditions, we have attempted to determine G-band homology from the following studies: Arrighi *et al.*, 1976; Baker *et al.*, 1979, 1983a; Baker and Barnett, 1981; Elder, 1980; Engstrom and Bickham, 1982; Greenbaum *et al.*, 1978a, b; Greenbaum and Baker, 1978; Haiduk *et al.*, 1979; Koop *et al.*, 1983; Maia and Hulak, 1981; Mascarello *et al.*, 1974a, b; Mascarello and Warner, 1974; Mascarello and Hsu, 1976; Pathak *et al.*, 1973; Robbins and Baker, 1980, 1981; and Yates *et al.*, 1979. Not all of these investigators used the same chromosomal numbering systems, therefore, in order to assimilate the different studies, we have used the standardized *Peromyscus* numbering system to imply homology. In several of the above studies (such as *Sigmodon*, Elder, 1980 and *Ochrotomys*, Engstrom & Bickham, 1982) the amount of homology that could be identified was such that comments on the origin of rearrangements in these taxa would be speculative. Using the above published accounts as well as other species banded in our laboratory, we have determined the following about the derived G-band conditions seen in Figure 1.

Chromosome 1 in *Peromyscus boylii* varied from the ancestral form in that it had a euchromatic short-arm addition (translocation) to the centric region. This rearrangement appeared in all 18 species of *Peromyscus* thus far G-banded (Robbins & Baker, 1981) and in *Onychomys* (Baker *et al.*, 1979). In *Oryzomys capito*, chromosome 1 varied from the ancestral form by the centromere position, with a heavy dark band immediately adjacent to the centromere. This condition was present in some but not all species of *Oryzomys* (Haiduk *et al.*, 1979). We have not found the primitive condition of chromosome 1 in any of the *Oryzomys* thus far examined. It is interesting to note that in *Baiomys taylori* and *Reithrodontomys* (Robbins & Baker, 1981; Yates *et al.*, 1979) chromosome 1 was identical to that proposed as primitive for Cricetidae. In *Onychomys* and *Peromyscus*, however, chromosome 1 appears to be a synapomorphy, which documents that these two genera shared a common

ancestor after separating from *Baiomys*, *Reithrodontomys*, *Neotoma*, and *Oryzomys*. Further, this synapomorphy documents the common ancestry of the 18 species of *Peromyscus* examined by Robbins and Baker (1981), an arrangement questioned by the conclusions of Carleton (1980).

The primitive condition of chromosomes 2 and 3 as determined in this paper have also been found in *Neotoma micropus* (Mascarello *et al.*, 1974b), *Reithrodontomys fulvescens* (Robbins & Baker, 1980), *Baiomys taylori* (Yates *et al.*, 1979), and *Onychomys leucogaster* and *O. torridus*, although in *Onychomys* there were additional heterochromatic short arms present (Baker *et al.*, 1979). The heterochromatic short arm on chromosome 3 of *Neotoma micropus* (Fig. 1) appears to be a populational variant (Mascarello & Warner, 1974).

In chromosome 4 the change in centromere position in *Oryzomys capito* shown in Figure 1 was also present in *Oryzomys palustris*, *O. melanotis* (Haiduk *et al.*, 1979), and *O. caudatus*, (chromosome 4 was fragmented in *O. delicatus*, *O. concolor*, and *O. bicolor*; Baker *et al.*, 1983a). This suggests that the change in centromere position may be a synapomorphic character for the genus *Oryzomys*. The proposed primitive condition of chromosome 4 was also found in *Reithrodontomys* (Robbins & Baker, 1980), *Onychomys* (Baker *et al.*, 1979), and *Baiomys* (Yates *et al.*, 1979).

The 5/6 fusion in *Oryzomys capito* (Fig. 1) may represent a synapomorphic condition for *O. capito* and an undescribed species (Baker *et al.*, 1983a), because the primitive condition of chromosome 5 was found in *O. melanotis* and *O. palustris* (Haiduk *et al.*, 1979) as well as in *O. delicatus* and *O. caudatus* (Baker *et al.*, 1983a). The proposed primitive condition of chromosome 5 was also found in *Baiomys taylori* (Yates *et al.*, 1979), *Reithrodontomys fulvescens* (Robbins & Baker, 1980), and *Onychomys torridus* (Baker *et al.*, 1979).

The proposed primitive conditions of chromosomes 6, 7, 8, 9, 10, 11, 12, 13, and 14 are also found in *Reithrodontomys fulvescens* (Robbins & Baker, 1980) and *Baiomys taylori* (Yates *et al.*, 1979). In *Oryzomys*, the primitive condition of chromosome 6 has not been found in any species examined. The derived condition of chromosome 11 found in *Oryzomys capito* was also found in several other species of *Oryzomys* (*O. melanotis*, *O. concolor*, *O. palustris*, and *O. bicolor*; Baker *et al.*, 1983a).

This could indicate that this is a synapomorphic condition for members of the genus *Oryzomys*.

In Figure 2 we have summarized an evolutionary scheme determined from a cladistic analysis of G-banded sequences. When we consider the 14 largest autosomal pairs (elements with sufficient G-band resolution to be relatively sure of homology), there have been as few as 4 major chromosomal changes that could explain the difference between the proposed ancestral G-band sequence of the Cricetidae complex and the proposed primitive condition for *Peromyscus*. This compares to 13 events (in the 14 largest autosomal pairs) that have occurred between the congeneric species *Peromyscus boylii* and *Peromyscus maniculatus* (Robbins & Baker, 1981). As few as 3 chromosomal events could explain the difference between the proposed ancestral G-band sequence of Cricetidae and the proposed primitive karyotype for the genera *Reithrodontomys*, *Neotoma*, and *Baiomys*. Within these genera, species often differ by more than 3 events (Baker *et al.*,

1979; Robbins & Baker, 1980, 1981; Mascarello & Hsu, 1976).

The chromosomal variation within *Oryzomys* is evident based on range in diploid number (*Oryzomys capito* $2n = 52$ FN = 62; *Oryzomys albigularis* $2n = 66$ FN = 86, $2n = 66$ FN = 112, $2n = 80$ FN = 92, Gardner & Patton, 1976; *Oryzomys subflavus* $2n = 46$ FN = 56, and Maia & Hulak, 1981) and variation in G-band pattern (Baker *et al.*, 1983a). For example, between populations of *Oryzomys albigularis*, at least 13 events must have occurred in order to account for the variation in fundamental number in the two $2n = 66$ cytotypes. Basically, it appears that the radiation that gave rise to the different genera was accompanied by little chromosomal evolution, whereas, within modern genera, speciation has often been accompanied by greater amounts of chromosomal evolution.

When we compared the types of chromosomal changes found within the various lineages, we also noted a nonrandom distribution of types of chro-

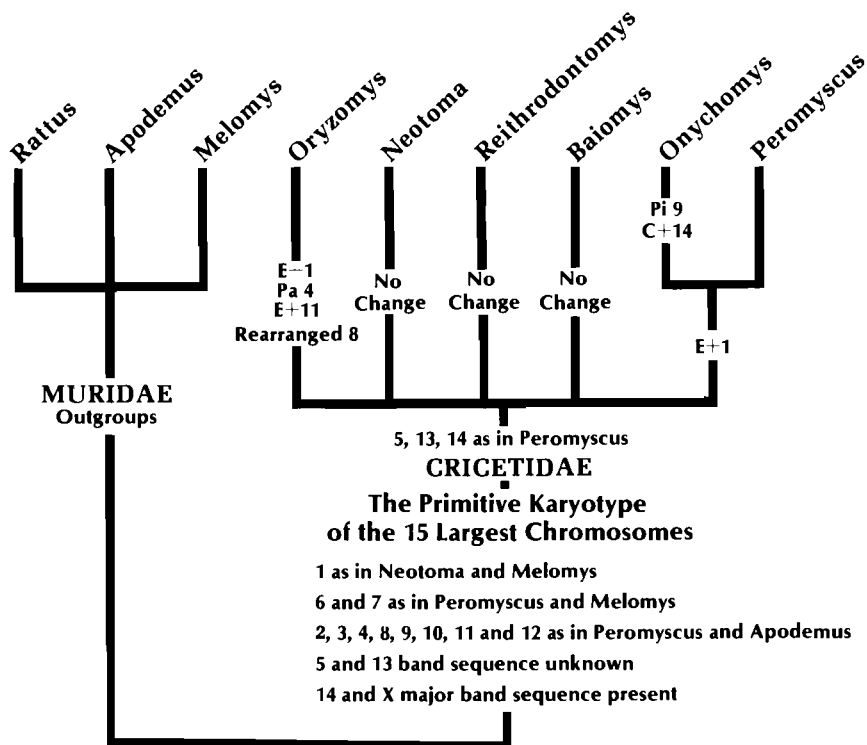


Fig. 2. The cladistic relationships of the proposed primitives for the genera *Peromyscus*, *Onychomys*, *Reithrodontomys*, *Baiomys*, *Neotoma* and *Oryzomys* based on the largest 14 G-banded chromosomal pairs. E + equals euchromatic addition; Pi equals presumed pericentric inversion; Pa equals paracentric inversion; C + equals heterochromatic arm addition; E - equals euchromatic loss.

mosomal rearrangements. A good example of this phenomenon is revealed by comparing the peromyscine group with the *Oryzomys* group of the family Cricetidae. Both groups contain a large number of species and occupy extensive ranges in North and South America, respectively. Within the peromyscine group, no centric fission-fusion events have been reported in 18 species of *Peromyscus* (Robbins & Baker, 1981) or 3 species of *Onychomys* (Baker *et al.*, 1979), whereas, within *Oryzomys*, eleven centric fission-fusion events have been documented by Maia and Hulak (1981), Koop *et al.* (1983) and many more have been inferred by Gardner and Patton (1976). Within *Peromyscus* and *Onychomys* over 60 heterochromatic arm additions have been documented by Baker *et al.* (1979), Baker and Barnett (1981), and Robbins and Baker (1981), yet none have been found in the autosomal chromosomes of *Oryzomys* (Haiduk *et al.*, 1979; Maia & Hulak, 1981; Koop *et al.*, 1983). Although only eleven species of *Oryzomys* have been examined, the initial findings show no evidence of heterochromatin other than that associated with the centromeric regions and sex chromosomes. The lack of centric fusion-fission events and abundance of heterochromatic arms in *Peromyscus* and *Onychomys* is contrasted with the abundance of centric fusion-fission events and lack of heterochromatic arms in *Oryzomys*. Clearly, between genera, a non-random distribution of chromosomal events is evident. These observations support the phenomenon of karyotypic orthoselection as defined by White (1975) and indicate that the specifics of chromosomal evolution in one group may not be applicable to other groups.

Relative to a primitive diploid number for the Cricetidae and Muridae, the species shown in Figure 1 had a $2n$ ranging from 42 to 54 (*Neotoma micropus* $2n=52$, *Peromyscus boylii* $2n=48$, *Oryzomys capito* $2n=54$, *Apodemus sylvaticus* $2n=48$, *Rattus norvegicus* $2n=42$, and *Melomys burtoni* $2n=48$). In the karyotypes examined, almost all chromosomes were acrocentric. The evidence appears to support the hypothesis that the 14 largest autosomal pairs were acrocentric in the primitive forms, which is compatible with Baker and Mascarello's (1969) proposal that a diploid number between 48 and 52 consisting of mostly acrocentric elements is the most likely primitive karyotypic condition for the cricetids. We suggest

that a $2n = 48-54$ may well encompass the primitive condition for Cricetidae and Muridae and that this diploid number will likely prove to encompass the primitive condition for most genera in these families.

The one hundred genera and over five hundred species in the family Cricetidae document the extensive morphological radiation that is found within this family. Despite this morphological radiation, it appears that many chromosomal G-band sequences have been conserved. Clearly, the magnitude of radiation in skeletal morphology among the six genera (*Rattus*, *Apodemus*, *Melomys*, *Neotoma*, *Oryzomys*, and *Peromyscus*) is a fairly representative sample of that found to distinguish major lineages within the two families. Yet few chromosomal differences distinguish the most probable primitive condition for the various genera. When this pattern of 'conservative chromosomal evolution with the associated magnitude of morphological change' is compared to the 'extensively rearranged euchromatic pattern seen in the two sibling species, *Reithrodontomys megalotis* and *R. montanus*' (Robbins & Baker, 1980), it is obvious that in these rodents there are examples where magnitude of chromosomal evolution and magnitude of morphological evolution are not positively correlated as suggested by Bush *et al.* (1977).

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