

PHYLOGENETIC RELATIONSHIPS OF *NYCTOMYS*
AND *XENOMYS* TO OTHER CRICETINE GENERA
BASED ON DATA FROM G-BANDED CHROMOSOMES

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ABSTRACT—Data from G-banded chromosomes are used to examine the relationships of *Nyctomys sumichrasti* and *Xenomys nelsoni* to rodents of the neotomine-peromyscine group. *Nyctomys* ($2n = 52$) has a G-banded karyotype essentially like that of *Neotoma micropus*. Chromosomal characters shared between *Nyctomys* and *Neotoma* are most likely the result of conserved primitive chromosomal arrangements. *Nyctomys* appears to have been derived early from the neotomine-peromyscine line after that line diverged from the South American cricetines. *Xenomys nelsoni* ($2n = 48$) possesses a G-banded karyotype that includes a banded chromosome 1 and is much like the karyotypes found in species of *Onychomys* and *Peromyscus*. If the banded condition of chromosome 1 is a synapomorphy for *Onychomys* and *Peromyscus* as has been proposed, then *Xenomys* should be included in this group rather than with *Neotoma*. However, the evolution of chromosome 1 is not clear, and the banded condition may be either primitive or due to convergence.

RESUMEN—Estudios de los cromosomas de *Nyctomys sumichrasti* y *Xenomys nelsoni* son usados para examinar las relaciones entre las dos especies y los miembros del grupo neotomine-peromyscine. El cariotipo de *Nyctomys* ($2n = 52$) es semejante al de *Neotoma micropus*, mientras el cariotipo de *Xenomys* ($2n = 48$) es similar a los de especies de los generos *Peromyscus* y *Onychomys*. Con estos datos, algunas conclusiones se pueden derivar. Primero, la similitud entre los cariotipos de *Nyctomys* y *Neotoma* sugiere una relacion cercana entre los dos generos, pero tambien es posible que la similaridad de los cariotipos sea resultado de características primitivas retenidas. Además, se considera que *Nyctomys* representa un linaje antiguo que fue derivado antes de el grupo neotomine-peromyscine y despues de los cricetine de America del Sur. Por otro lado, la similitud entre los cariotipos de *Xenomys*, *Onychomys*, y *Peromyscus* (especialmente respecto al cromosoma 1) indica posiblemente una relacion cercana entre estos tres generos, parece que fueron derivados de un antecesor comun. Sin embargo, es posible que estas características sean primitivas o convergentes, y por ahora es difícil decidir entre las conclusiones propuestas.

The monotypic rodent genera *Nyctomys* and *Xenomys* have long been considered members of the Neotropical cricetine assemblage. The phylogenetic relationships of these two genera to each other and to other Neotropical cricetines, however, have remained uncertain. Hershkovitz (1962) included *Nyctomys* with the South American cricetines of the thomasomyine group (*Thomasomys* and *Rhipidomys*). Alternatively, Burt (1960) concluded that there was a strong *Neotoma-Nyctomys* affinity. Hooper and Musser (1964) hypothesized that *Nyctomys* represented a phylogenetic outlier relative to both the South American and the neotomine-peromyscine cricetines. They proposed that *Nyctomys* be removed from the thomasomyine group and be recognized as a primitive outlier, intermediate in taxonomic position to both the South American and the neotomine-peromyscine cricetines. Voss and Linzey (1981) reached conclusions similar to those of Hooper and Musser (1964) and proposed

that *Nyctomys* be considered outside all the proposed subunits of the family Muridae (includes the Cricetidae). Carleton (1980) found many similarities between *Nyctomys* and the *Tylomys-Otodylomys* group, again suggestive of the retention of primitive characters and possibly an early divergence of *Nyctomys* from other cricetines.

The systematic position of the genus *Xenomys* has been debated less in the literature. Hooper (1960) noted similarities between *Xenomys* and *Neotoma alleni*. Hooper and Musser (1964) included *Xenomys* within the neotomine-peromyscine group. Carleton (1980) included *Xenomys* as an early off-shoot of the lineage that gave rise to *Neotoma* and suggested that *Xenomys* shared a common ancestor with *Hodomys* after diverging from the *Neotoma* lineage. In the present paper, data from G- and C-banded chromosomes of *Nyctomys sumichrasti* and *Xenomys nelsoni* are evaluated to further examine the systematic and evolutionary relationships of these taxa.

MATERIALS AND METHODS—All specimens examined were live-trapped from natural populations. Some animals were stressed with yeast (Lee and Elder, 1980), and bone marrow was processed in the field. A suspension of bone marrow cells in fixative was then frozen in liquid nitrogen as described by Baker et al. (1982) and returned to the laboratory where slides were prepared for G- and C-banding. Live individuals were also transported to the laboratory and processed both by the yeast stress-bone marrow and tissue culture methods. Reference samples of cultured cells were suspended in media supplemented with DMSO (Baker and Qumsiyeh, in press) and are stored in liquid nitrogen in the Vital Tissue Collections, Texas Tech University. The procedure of Seabright (1971) was used for G-banding and those of Stefos and Arrighi (1971) were used for C-banding. The standardized numbering system for *Peromyscus* chromosomes (Committee for Standardization of Chromosomes of *Peromyscus*, 1977) was used to indicate proposed homology. The G-banded karyotype of *Neotoma micropus* and *Peromyscus boylii* ($2n = 52$) were compared to *Nyctomys* and *Xenomys*. The karyotype of *N. micropus* and *P. boylii* ($2n = 52$) have been proposed as retaining the primitive autosomal conditions for their respective genera (Mascarello and Hsu, 1976; Koop et al., 1985), and the banding pattern of the larger chromosomes of *N. micropus* has been proposed as being primitive for the cricetid complex of rodents (Koop et al., 1984).

Specimens examined were prepared as voucher specimens and deposited in The Museum, Texas Tech University. Individuals of *N. sumichrasti* (4 males) and *X. nelsoni* (2 males, 1 female) were collected from Mexico (6 km SE Chamela, Jalisco).

RESULTS—The G-banded chromosomes of *N. micropus* and *Nyctomys* are shown in Fig. 1. Consistently detectable differences that distinguish the karyotypes of these two species include a previously reported (Mascarello and Warner, 1974; Mascarello and Hsu, 1976) polymorphism for a heterochromatic short arm on pair 3 of *Neotoma* (no such heterochromatic addition was present in our sample of *Nyctomys*) and an apparent rearrangement in chromosome 2. Chromosome 2 of *Nyctomys* is smaller than its proposed homologue in *Neotoma*.

A composite comparison of the haploid complements of *Peromyscus boylii* ($2n = 52$) and *Xenomys nelsoni* is shown in Fig. 2. *Peromyscus boylii* ($2n = 52$) has a karyotype like that proposed as primitive for the genus *Peromyscus* (Robbins and Baker, 1981). Chromosomes 2, 5, and 11 of *Xenomys* have euchromatic short arms and, therefore, differ from the proposed primitive for *Peromyscus* by presumed pericentric inversions. Additionally, chromosomes 8 and 22 of *Xenomys* differ from the proposed

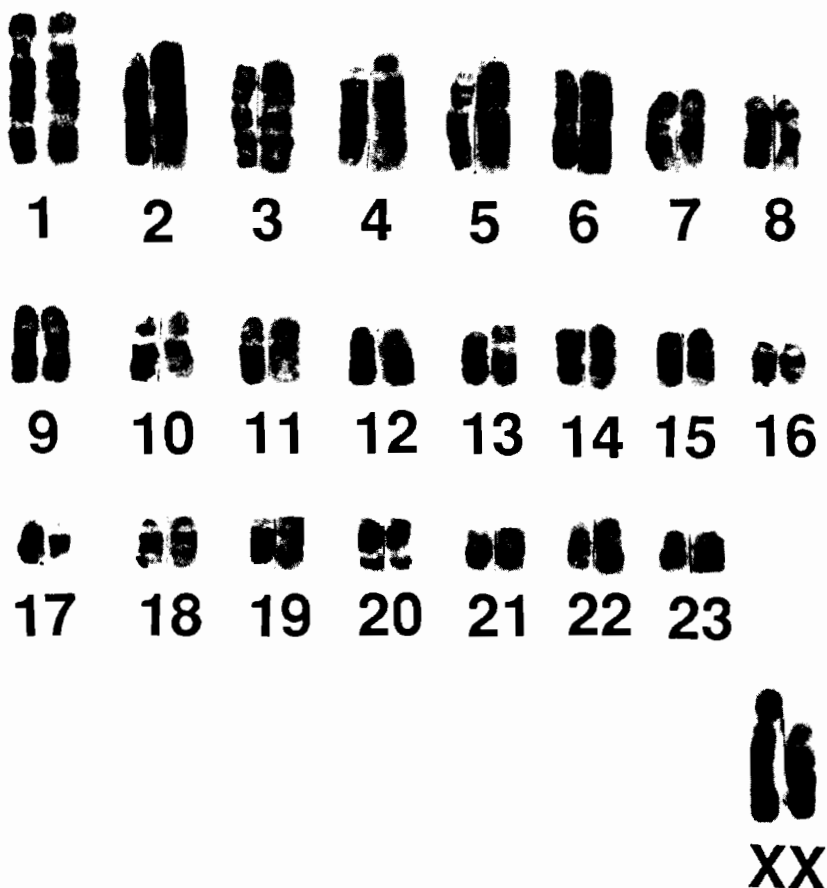


FIG. 1.—Comparison of the G-banded haploid chromosomal complements of *Neotoma micropus* (chromosome on the left of each homologous pair) and *Nyctomys sumichrasti* (chromosome on the right).

primitive for *Peromyscus* by rearrangement events of unknown origin. Except differences in the size of the short arms of the X chromosome, the remainder of the chromosomal complement appears to be identical in both species.

DISCUSSION—The overt similarity of the G-banding patterns of *Nyctomys* and *Neotoma* is compatible with the systematic conclusions of Burt (1960), Hooper and Musser (1964), Carleton (1980) and Voss and Linzey (1981). Some caution should be exercised in interpreting these data, however. Mascarello and Hsu (1976) and Koop et al. (1985) suggested that the primitive karyotype for *Neotoma* was probably like that found in *N. micropus*, and Koop et al. (1984) hypothesized that many of the chromosomal character states found in the G-band karyotype of *N. micropus* were primitive for all

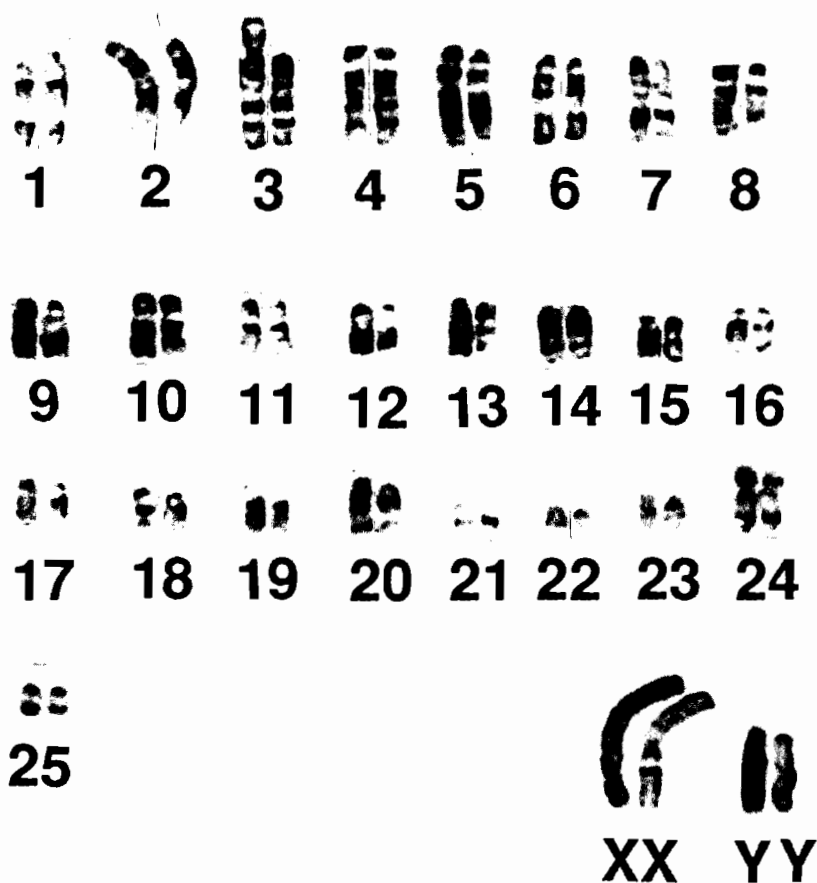


FIG. 2—Composite comparison of a haploid set of the G-banded chromosomes of *Peromyscus boylii* and *Xenomys nelsoni*. The chromosome on the left of each pair is from *P. boylii*; that on the right is from *X. nelsoni*.

New World cricetines. Therefore, the G-band patterns shared by *N. micropus* and *Nyctomys* may not document a common ancestry for these taxa after their divergence from the remainder of the New World cricetines but rather represents a retention of the primitive condition. Also, the genus *Nyctomys* contains some chromosomal variation; at least one other cytotype is known ($2n = 50$, $fn = 52$; Lee and Elder, 1977). The specimens studied by Lee and Elder (1977) were collected from the same locality as our four specimens. Data from banded chromosomes are not available for the $2n = 50$ cytotype, however, so its relationship to the $2n = 52$ is presently unclear.

The biarmed conditions of chromosome pairs 22 and 23 may by synapomorphic for the peromyscine-neotomine clade within the Cricetidae. There is a further possibility that a diploid number of 52 with a G-band pattern as seen in *Nyctomys* and *Neotoma* may contain synapomorphies for

the neotomine clade. The South American cricetines for which chromosomal banding data are available (*Oryzomys*, *Neacomys*, *Nectomys*, *Holochilus*, and *Sigmodon*) do not have chromosomal synapomorphies that unite them to the exclusion of other members of the family. However, within these genera there are several autapomorphic euchromatic rearrangements (Baker et al., 1983). That *Nyctomys* shares none of the apomorphic arrangements found in the South American species thus far examined (Baker et al., 1983) suggests that *Nyctomys* did not share a recent common ancestry with these South American taxa. The chromosomal data suggest that *Nyctomys* may represent either an offshoot of the neotomine lineage (retaining the plesiomorphic karyotype), or it may represent a lineage independently derived from the cricetid common ancestor that retains primitive chromosomal characters as described by Koop et al. (1984, 1985).

From a chromosomal standpoint, *Xenomys* is no more different from some species of *Peromyscus* than some species of *Peromyscus* are from each other (Robbins and Baker, 1981; Rogers et al., 1984; Stangl and Baker, 1984). Unfortunately, there is not a chromosomal synapomorphy that clearly distinguishes the genus *Peromyscus* from all other cricetine genera. However, biarmed chromosomes 1, 22, and 23 (Baker et al., 1979; Baker and Barnett, 1981; Rogers, 1983; Engstrom and Bickham, 1983) have been interpreted as synapomorphies for all species of *Peromyscus* and *Onychomys*. The biarmed condition of chromosomes 1 and 23 is also present in *Xenomys*, suggesting that it shared a common ancestry with the *Peromyscus-Onychomys* lineage after diverging from other cricetines. The other rearrangements in *Xenomys* (chromosomes 2, 5, 8, 11, and 22) appear to be either autapomorphies for *Xenomys* or retained primitive characters as seen in *Neotoma*. Convergent chromosomal evolution has been documented in peromyscines (Robbins and Baker, 1981; Rogers, 1983; Hood et al., 1984; Stangl and Baker, 1984), and clades that are identified by highly variable chromosomes are suspect until verified by synapomorphies from other studies (Haiduk and Baker, 1982; Baker et al., 1983; Baker et al., 1987).

The relationships based on chromosomal data are that *Nyctomys* has an unresolved relationship to *Neotoma*. *Xenomys* is placed with *Onychomys* and *Peromyscus*, and, based solely on chromosomal data, the three form an unresolved trichotomy. The placement of *Xenomys* at this position in an evolutionary tree of cricetine evolution clade disagrees with the previous conclusions of Carleton (1980). If the relationships proposed by Carleton (1980) are correct, the chromosomal characters shared between *Xenomys* and *Peromyscus* (for example a diploid number of 48 and a euchromatic biarmed 1) either represent convergences, having been derived independently in both the *Neotoma* clade and the *Onychomys-Peromyscus* clade, or represent the primitive condition for the entire peromyscine-neotomine clade.

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