

# PHYLOGENETIC ANALYSIS OF KARYOLOGICAL VARIATION IN THREE GENERA OF PEROMYSCINE RODENTS

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## Abstract

Yates, T. L., R. J. Baker, and R. K. Barnett (Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, Texas 79409) 1979. *Phylogenetic analysis of karyological variation in three genera of peromyscine rodents*. *Syst. Zool.* 28:40-48.—Chromosomal homologies between *Neotomodon alstoni*, *Baiomys taylori* and species of *Peromyscus* for which G-band chromosomal data are available in the literature were identified using G- and C-banding techniques. The primitive karyotype for the peromyscine genera is hypothesized to have a  $2n = 48$  composed of two or three pairs of biarmed and 20 to 21 pairs of acrocentric autosomes, with heterochromatin restricted to the centromeric regions. Patterns of chromosomal change are presented in the form of a cladogram. The G-banded karyotype of *Baiomys taylori* is composed of all acrocentric autosomes and is most like that of *Peromyscus crinitus*, differing only by pericentric inversions in pairs 1, 22, and 23. *Neotomodon alstoni* shares synapomorphic inversions with several species of *Peromyscus*. Based on these data, we believe *Neotomodon* is best considered a congener of *Peromyscus*. [*Peromyscus*; *Neotomodon*; *Baiomys*; karyology; phylogenetic relationships.]

Certain types of chromosomal data are particularly well suited to a cladistic approach for the following reasons. Chromosomal changes occur as distinct events and, by using G-band analysis, it is possible to determine which chromosomes are homologous among closely related taxa and which chromosomes have changed. By observing the overall pattern, plus outgroup comparisons, one can often determine which chromosomal condition is primitive (plesiomorphic) and which is derived (apomorphic). Knowledge of the primitive and derived karyotypic conditions allows the inference of phylogenetic relationships and construction of a phylogeny based on synapomorphic (derived character states shared between species) chromosomal changes. Certain types of chromosomal changes are rare (for instance, pericentric inversions) and the probability that the same event would occur twice (convergent evolution) is unlikely. Thus, species which share derived conditions probably evolved from a common ancestor which contained the derived conditions.

The genus *Peromyscus* is an excellent taxon for chromosomal studies because: 1) there are many species (57 recognized

by Hooper, 1968) from which data can be gathered; 2) several species are represented by numerous geographic races, a condition which permits correlation with low-level chromosomal differentiation; 3) individuals are small and relatively easy to collect; 4) they readily breed in the laboratory and, in some cases, fertile hybrids can be produced; 5) all species thus far examined have a diploid number of 48, yet there is considerable variation in the gross morphology of the karyotype (intraspecific and interspecific); 6) there are enough pericentric inversions to establish synapomorphy patterns; 7) there is considerable variation in heterochromatin between species and populations, and 8) cell lines grow well in tissue culture and detailed cytogenetic studies can be made. For these and other reasons, numerous authors have examined chromosomal variation in *Peromyscus* (Hsu and Arrighi, 1968; Duffey, 1972; Lee et al., 1972; Pathak et al., 1973; Schmidly and Schroeter, 1974; Arrighi et al., 1976; Murray and Kitchin, 1976; Greenbaum and Baker, 1978; Greenbaum et al., 1978a and 1978b).

Baker and Mascarello (1969) suggested that the primitive karyotypic condition

for the subfamily Cricetinae was largely composed of acrocentric elements. Bowers et al. (1973) and Greenbaum et al. (1978b) hypothesized that the primitive karyotype for the *Peromyscus maniculatus* group of the subgenus *Peromyscus* was composed of nearly 30 acrocentric elements. Lawlor (1974), however, argued that acrocentric elements represent a derived condition in the genus *Peromyscus*.

Recent G- and C-band chromosome data (Greenbaum and Baker, 1978) support the hypothesis that the primitive karyotype for the *maniculatus*-group was composed of a large number of acrocentric elements (near 30). After a comparison of the G- and C-band chromosomal data for *P. melanotis*, *P. polionotus*, *P. maniculatus* and *P. floridanus*, these authors concluded that *P. melanotis*, with 30 acrocentric elements, represented the least derived of the karyotypes of the three *maniculatus*-group species thus far studied. They concluded that the *melanotis* karyotype was plesiomorphic for the *maniculatus*-group.

Greenbaum and Baker (1978), additionally, found the *P. melanotis* karyotype to contain the least amount of C-band positive material and the *maniculatus* karyotype to contain the most. They concluded that the evolutionary trend in the *maniculatus*-group was to increase the amount of heterochromatin and the number of banded elements (by pericentric inversions and by heterochromatic short arm additions). Based on this apparent trend and data from other species, they suggested that *P. crinitus*, which has little heterochromatin and 40 acrocentric autosomes, may have retained a karyotype most like that primitive for the genus *Peromyscus*.

If the inferences of Greenbaum and Baker (1978) are correct, then the sister-group of *Peromyscus* should also have had a primitive karyotype composed of all, or mostly all, acrocentric elements with only centromeric heterochromatin. Critical tests of this prediction would require outgroup comparisons by examin-

ing the G- and C-banding patterns of other genera believed to be closely related to *Peromyscus*. If the G-banding patterns of the acrocentric chromosomes of the species differ from their corresponding banded counterparts in *Peromyscus* by a pericentric inversion (especially in certain chromosomes which may have been banded or acrocentric in the primitive) and only exhibit heterochromatin at the centromeric regions, this would be strong evidence for an essentially acrocentric primitive karyotype for *Peromyscus*.

The peromyscines include the genera *Baiomys*, *Scotinomys*, *Ochrotomys*, *Neotomodon*, *Peromyscus*, *Reithrodontomys* and *Onychomys* (Hooper and Musser, 1964a). Of these genera, *Peromyscus* has been said to be most closely related to *Reithrodontomys* and *Neotomodon*, and most distantly related to *Baiomys* and *Scotinomys* (Packard, 1960; Hooper and Musser, 1964b). Species of *Reithrodontomys*, however, do not exhibit a common diploid number of 48. Therefore, we selected *Neotomodon*, which does have a  $2n = 48$ , as the nearest relative to *Peromyscus*, and *Baiomys* ( $2n = 48$ , Hsu and Benirschke, 1967, and Lee et al., 1977) as a more distant relative for outgroup comparison. This paper presents data on G- and C-bands of *Baiomys* and *Neotomodon* and discusses the phylogenetic and evolutionary implications of these data.

#### METHODS AND MATERIALS

All preparations were from fibroblast tissue cultured cells initiated from lung biopsies. Cultures were grown at 37°C in Ham's F-10 medium supplemented with 11 percent fetal calf serum. Velban (Lilly) was used as a mitotic inhibitor (one drop, .01 percent to 15 ml media, for 15 minutes). Methods of G- and C-chromosome banding were described by Greenbaum et al. (1978a). G-banded chromosomes are numbered and arranged according to the proposed standardized karyotype for the genus *Peromyscus* (Committee, 1977). Several banded karyotypes (at least five) were prepared for each specimen examined, and homologies were determined

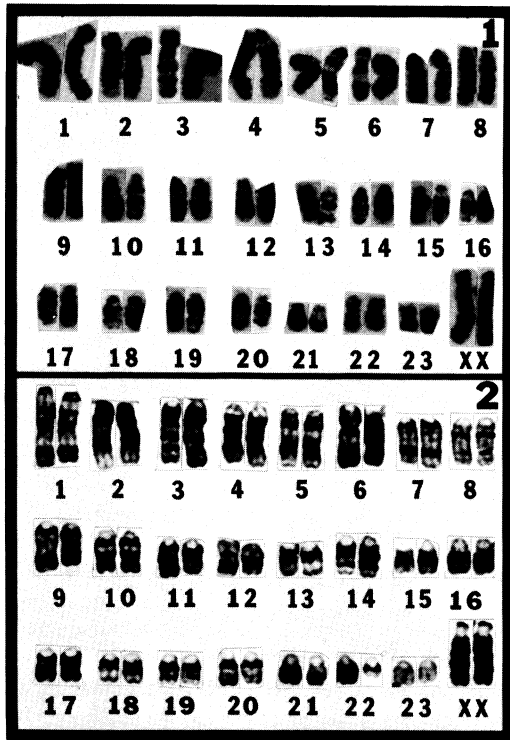


FIG. 1.—G-banded karyotype of *Neotomodon alstoni*. Homologous pairs in this and subsequent figures are numbered according to the standard *Peromyscus* karyotype (Committee, 1977).

FIG. 2.—G-banded karyotype of *Baiomys taylori*.

based on side-by-side comparison of differential longitudinal staining patterns of each chromosome. Only spreads with the diploid number characteristic of the species were used in the comparisons.

Specimens examined were as follows: *Neotomodon alstoni* (2): Mexico: Distrito Federal, 1 km N Morelos—D.F. Border, Hwy. 95 (F<sub>1</sub>s of wild trapped individuals). *Baiomys taylori* (2): Mexico: Queretaro, 3 km N Jalpan. *Peromyscus melanotis*: as reported by Greenbaum et al., 1978a. *P. crinitus*: as reported by Pathak et al., 1973.

#### RESULTS

*The Neotomodon alstoni karyotype.*—G-banded karyotypes for *Neotomodon* and *Baiomys* are shown in Figs. 1 and 2, and C-banded results for *Neotomodon*

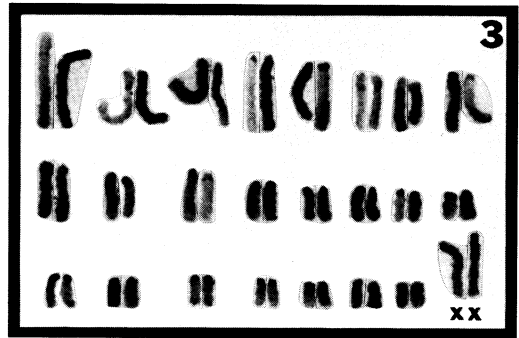


FIG. 3.—C-banded karyotype of *Neotomodon alstoni*.

are shown in Fig. 3. Specimens of *Neotomodon alstoni* examined have a diploid number of 48, with 30 acrocentric and 16 biarmed autosomes. The sex chromosomes are biarmed.

The C-banded karyotype (Fig. 3) reveals centromeric heterochromatin for all autosomes but no C-band positive short arm associations. The X chromosome in the *Neotomodon alstoni* examined was a large subtelocentric of which the short arms stain C-band positive. The short arm of the X is much smaller than in *Peromyscus melanotis* and is closer in size to that reported for *P. maniculatus* (Greenbaum et al., 1978a).

*The Baiomys taylori karyotype.*—Both specimens of *Baiomys taylori* examined had a karyotype consisting of 48 acrocentric chromosomes (Fig. 2). The C-banded karyotype reveals only centromeric heterochromatin.

*Intergeneric homology.*—Figures 4 and 5 are composite karyotypes comparing G-banded chromosomes of *Peromyscus melanotis*, *Neotomodon alstoni*, and *Baiomys taylori*. Each trio consists of a *P. melanotis* chromosome on the left with what we interpret as the homologous element of *N. alstoni* in the middle and the corresponding homolog of *B. taylori* on the right. Using G- and C-banding techniques, we believe we have identified homologous elements for all 48 chromosomes between all three genera. The following discussion is based on the pre-

sumed homology of elements as shown in Figs. 4 and 5. From the chromosomes shown in Figs. 4 and 5, plus other spreads, we have concluded that the karyotypes of *P. melanotis*, *N. alstoni*, and *B. taylori* are related as follows.

Fourteen pairs of acrocentric autosomes are homologous and unchanged in G- and C-banding patterns among the three taxa (Fig. 4). The euchromatic portions of the X chromosomes are homologous and unchanged in G-banding patterns (Fig. 4). The X in *P. melanotis* and *N. alstoni* have heterochromatic short arm associations which are lacking in *B. taylori*.

Seven pairs of autosomes (pairs 1, 2, 3, 6, 9, 22 and 23) are biarmed and show identical banding patterns between *P. melanotis* and *N. alstoni*, but appear to differ from the corresponding acrocentric condition in *B. taylori* by a pericentric inversion (Fig. 5). Chromosome 7 is acrocentric in *P. melanotis* and *B. taylori* and differs from the homologous biarmed element in *N. alstoni* by a pericentric inversion. Chromosome 20 is acrocentric in *B. taylori* and *N. alstoni* and differs from the metacentric chromosome 20 of *P. melanotis* by pericentric inversion.

#### DISCUSSION

When this study began, we believed that an examination of representatives of *Baiomys* and *Neotomodon* would serve as the best outgroup comparison for determining the primitive karyotype for the genus *Peromyscus*. We now believe that this is the case with *Baiomys*, but chromosomal data strongly suggest that *Neotomodon* shares a number of synapomorphic characteristics with some members of the genus *Peromyscus* and its proper systematic position is a congener with *Peromyscus*. For this reason, in the following discussion we present the implications of *Baiomys* G-bands. Then we present why we feel that the most parsimonious explanation for the G-band pattern in *Neotomodon* is that *Neotomodon* is best considered congeneric with *Peromyscus*.

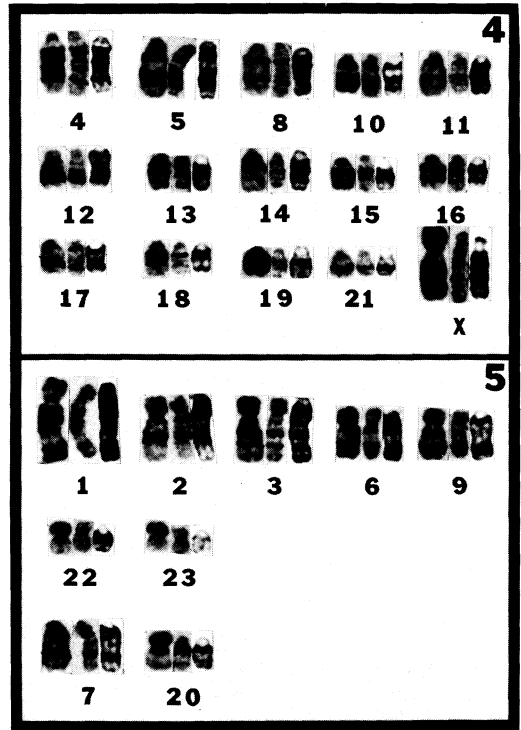


FIG. 4.—Composite partial G-banded karyotype comparing homologous elements of *Peromyscus melanotis*, *Neotomodon alstoni*, and *Baiomys taylori* showing elements which are unchanged between the species. Figs. 4–5 include the entire haploid complement for each of the three species. In these figures the first chromosome in each group of homologs is from *P. melanotis*, the second from *N. alstoni*, and the third from *B. taylori*.

FIG. 5.—Composite partial G-banded karyotype comparing homologous elements of *P. melanotis*, *N. alstoni*, and *B. taylori*. Pairs 1, 2, 3, 6, 9, 22 and 23 are acrocentric in *B. taylori* and biarmed in *P. melanotis* and *N. alstoni*. Pair 7 is biarmed in *N. alstoni* and acrocentric in *P. melanotis* and *B. taylori*. *P. melanotis* displays a biarmed condition for pair 20, whereas this element is acrocentric in the other two species. These differences are apparently the result of pericentric inversions.

#### *Comparison of the Baiomys taylori karyotype to other peromyscines*

The G-banded karyotype of *B. taylori* is most similar to the karyotype of *P. crinitus*. These two karyotypes differ in pairs 1, 22, and 23 by pericentric inversions. The high degree of similarity between these karyotypes can be explained

by 1) a close phylogenetic relationship for these species, 2) by the karyotypes being symplesiomorphic, or 3) by convergence. We do not interpret reason one as correct because morphology of the cranium and glans penis clearly shows that *Baiomys* is not as closely related to the species currently placed within the genus *Peromyscus* as these species are to each other (Packard, 1960; Hooper, 1959; Hooper and Musser, 1964b). These conclusions are reinforced by the fossil record which shows *Baiomys* as a distinct entity from *Peromyscus* as early as the Pliocene (Hibbard, 1953). Convergence is not likely to explain all of the similarity because independent convergent events (in this case, pericentric inversions) would be required in three pairs of homologous chromosomes. We interpret the similarity of the karyotypes of *Baiomys taylori* and *P. crinitus* as symplesiomorphy.

If the karyotypic characteristics shared by *P. crinitus* and *B. taylori* are symplesiomorphic, then one must strongly suspect that these elements were present in the primitive karyotype for the genus *Peromyscus*. Greenbaum and Baker (1978) suggested that in the primitive karyotype for the genus, pairs 1, 22, and 23 were biarmed, the morphology of pairs 2, 3, 6, and 9 was unknown, and the remainder were acrocentric. Pairs 2, 3, 6, and 9 are acrocentric in *B. taylori*, which suggests that these were acrocentric in the pre-*Peromyscus* line. Additional data which support the acrocentric condition for pairs 2, 3, 6, and 9 as primitive in pre-*Peromyscus* are available in Fig. 2 of Mascarello et al. (1974). They made a G-band comparison between *P. crinitus* and a species from the genus *Neotoma* (a neotomine genus), which is believed to be even less closely related to *Peromyscus* than is *Baiomys* (Hooper, 1968). They concluded that pairs 2, 3, 6, and 9 are acrocentric in *Neotoma micropus* and homologous in G-banding pattern to their counterparts in *P. crinitus* (see Mascarello et al., 1974, fig. 2). Elements on the top row of this figure relate to the stan-

dardized *Peromyscus* karyotype (Committee, 1977) as follows: X, 3, 2, 1, 4, 5, 6, 7, 9, and 10, respectively. If it is true that pairs 2, 3, 6, and 9 were acrocentric for the progenitor of *Peromyscus*, then the most parsimonious way to explain the available G-banding data for species of *Peromyscus* is to have pericentric inversions in 2, 3, 6, and 9 in the right hand lineage of fig. 9 of Greenbaum and Baker (1978). This means that pairs 2, 3, 6, and 9 are synapomorphic for the lineage that gave rise to *P. floridanus*, *P. gossypinus*, *P. leucopus*, and the *P. maniculatus* group.

Pairs 22 and 23 are biarmed (both arms euchromatic but, in some cases, heterochromatin has been added to the short arms; Greenbaum and Baker, 1978) in all species of *Peromyscus* thus far studied, whereas these pairs are acrocentric in *Baiomys taylori*. There are two small pairs which are biarmed in *Neotoma micropus* and, according to Mascarello et al. (1974:698, fig. 2), these elements have the same G-banding pattern as is characteristic of pairs 22 and 23 of *P. crinitus*. The most parsimonious explanation is that the biarmed condition was primitive for pairs 22 and 23 in the common ancestor of *Neotoma*, *Baiomys*, and *Peromyscus*, and that these elements underwent inversions from biarmed to acrocentric in the lineage that gave rise to *Baiomys taylori* after that lineage was separated from the *Peromyscus* stock.

The situation with pair 1 is more complicated. The difference between pair 1 of *P. crinitus* and *B. taylori* is a pericentric inversion. In *Neotoma micropus* pair 1 is acrocentric and identical, G-band for G-band, with the long arm of chromosome 1 of *P. crinitus*, but differs from pair 1 of *P. crinitus* by the absence of the short arm (not by a pericentric inversion, as is seen in *B. taylori*). Although different combinations of additions or deletions of heterochromatin, plus an inversion, explain the variation between the recognizable morphs of pair 1, we speculate that the condition of pair 1 in *Neotoma* is most likely primitive and there

has been an addition of material, as seen in *Peromyscus*, with this addition inverted in *Baiomys*. Some light may be shed on the primitive morphology of pairs 1, 22, and 23 by examining the G-band patterns of the chromosomes of *Baiomys musculus*, which has ten pairs of biarmed autosomes (Lee and Elder, 1977).

G- and C-banding data for *Baiomys taylori* support the hypothesis (Greenbaum and Baker, 1978) that the primitive karyotype for the genus *Peromyscus* consisted of mostly acrocentric elements and that the karyotype of *P. crinitus* is a likely candidate for the primitive condition. Based on our data on *B. taylori*, and the comparisons of Mascarello et al. (1975) of *Peromyscus* with *Neotoma*, we conclude that the primitive autosomal karyotype consisted of pairs 22 and 23 biarmed, the morphology of pair 1 unknown, with all others acrocentric. With the possible exception of pair 1 (see Pathak et al., 1973), the primitive karyotype contained only centromeric heterochromatin (Greenbaum and Baker, 1978). The proposed phylogenetic arrangement by Greenbaum and Baker (1978) for eight species of *Peromyscus* consisted of two possible major lineages. One sister group included *P. melanotis*, *P. polionotus*, *P. maniculatus*, *P. gossypinus* and *P. floridanus*. Our data suggest that this lineage has synapomorphic pericentric inversions in chromosome pairs 2, 3, 6, and 9. The remaining species, *P. crinitus*, *P. boylii*, and *P. eremicus* (Greenbaum and Baker, 1978), are characterized by essentially no rearrangement of the euchromatic autosomal complement except for a polymorphism for a pericentric inversion in pair 9 in *P. boylii*. As such, *P. crinitus* and *P. eremicus* have no synapomorphic characteristics, and therefore chromosomal data do not reveal their evolutionary position.

#### *Comparison of the Neotomodon karyotype to other peromyscines*

G-banding chromosomal homology indicates that the karyotype of *Neotomodon alstoni* is more like those of *P. gossypi-*

*mus*, *P. melanotis*, and *P. floridanus* than it is like the more plesiomorphic karyotypes of *Baiomys taylori* or *P. crinitus*. The presence of synapomorphic pericentric inversions in chromosome pairs 2, 3, 6, and 9 between *N. alstoni* and *P. melanotis*, *P. maniculatus*, *P. polionotus*, *P. gossypinus*, and *P. floridanus* indicates that these species of *Peromyscus* and *N. alstoni* shared a common ancestor after the inversions of chromosome pairs 2, 3, 6, and 9. The retention of the hypothesized primitive acrocentric condition for chromosome pairs 20 and 11 in *N. alstoni* suggests that *Neotomodon* diverged from this lineage prior to the synapomorphic inversion in pair 20 for the *maniculatus* group and the autapomorphic inversion in pair 11 in *floridanus*. The inversion that produced a biarmed pair 7 in *Neotomodon* probably occurred after the *N. alstoni* stock diverged from the lineage.

The affinity between *N. alstoni* and *P. floridanus* in chromosomal characteristics is also suggested in the characteristics of the soft and hard parts of the glans penis (Hooper and Musser, 1964a). Exomorphologically, *Neotomodon* closely resembles *Peromyscus*. If our interpretation of the chromosomal data are true, then *Neotomodon* and *Peromyscus* are congeneric.

Our interpretation of the evolutionary position of *B. taylori* and *P. alstoni* (*Neotomodon*) to other peromyscine rodents thus far examined is presented in Fig. 6. Karyotypic data for species of *Peromyscus* not examined in this study are after Greenbaum and Baker (1978). *Baiomys taylori* is distinguished from the genus *Peromyscus* by the presence of autapomorphic inversions in chromosome pairs 22, 23 and possibly 1. Based on the comparisons of Mascarello et al. (1974), Greenbaum and Baker (1978), and our data, the only possible synapomorphy for the genus *Peromyscus* is an inversion in pair 1. However, as discussed earlier, this may represent a plesiomorphy. *Peromyscus crinitus* and *P. eremicus* show no further synapomorphies and thus represent an unresolved trichotomy with all re-

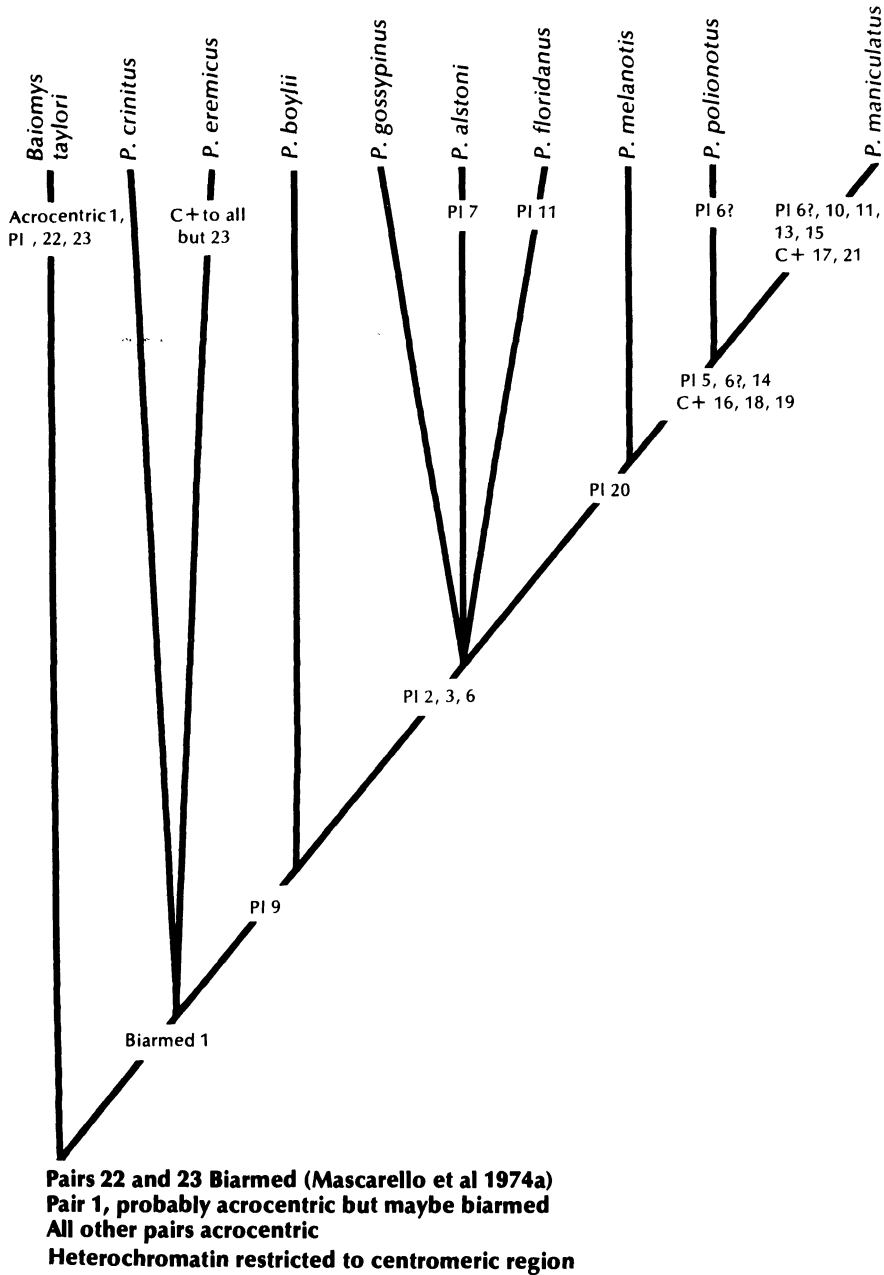


FIG. 6.—Cladogram showing relationship of *B. taylori* and *P. alstoni* (= *Neotomodon*) to other species of *Peromyscus* based on G-band chromosomal homologies. Breaks on main axis of diagram represent synapomorphies. Breaks in vertical lines indicate autapomorphies. G-band chromosomal data for species of *Peromyscus* not obtained in this study are after Greenbaum and Baker (1978).

maining species. *Peromyscus eremicus* does possess autapomorphic heterochromatic additions to all chromosomes except 23. *Peromyscus boylii* exhibits a polymorphic inversion in pair 9, which, in the biarmed condition, is indistinguishable from the condition found in the remaining species of *Peromyscus* presented in Fig. 6. The most parsimonious explanation for this is that the biarmed condition in *boylii* is a synapomorphy shared with *P. gossypinus*, *P. floridanus*, *P. alstoni* and those members of the *maniculatus*-group thus far examined. If this is the case, then *P. boylii* diverged from that lineage after the inversion in 9 but prior to the inversions in 2, 3, and 6, which are synapomorphies for the remaining species in that group, namely, *P. gossypinus*, *P. alstoni*, *P. floridanus*, *P. melanotis*, *P. polionotus* and *P. maniculatus*. *Peromyscus gossypinus* shows no additional changes, *P. alstoni* shows an autapomorphic inversion in pair 7, and *P. floridanus* exhibits an autapomorphic inversion in 11. As a result, these three species represent an unresolved tetratomy with the remaining lineage composed of *P. melanotis*, *P. polionotus*, and *P. maniculatus*. These last three species have a synapomorphic inversion for pair 20. *Peromyscus polionotus* and *P. maniculatus* possess synapomorphic inversions in pairs 5 and 14 and heterochromatic additions for pairs 16, 18 and 19. The condition of chromosome 6 is highly variable in these species and a discussion is not appropriate here (see Greenbaum and Baker, 1978). *Peromyscus maniculatus* can be distinguished by the presence of autapomorphic inversions in pairs 10, 11, 13 and 15 and heterochromatic additions to 17 and 21.

There are other interpretations of these data than those shown in Fig. 7. For instance, it is possible that the primitive condition for pairs 2, 3, 6, and 9 is biarmed, which would mean that *Baiomys* and *P. crinitus*, *P. boylii*, and *P. eremicus* would have synapomorphic character states. We feel this interpretation is less probable than that shown in Fig. 6

because of paleontological (Hibbard, 1953), cranial (Packard, 1960) and genitalic (Hooper and Musser, 1964b) data and because of chromosomal data from the genera *Neotoma* (Mascarello et al., 1974; Mascarello and Hsu, 1976) and *Onychomys* (Baker et al., 1979). In fact, if pairs 2, 3, 6, and 9 were primitively biarmed then *Neotoma* and *Onychomys* would have synapomorphies with *Baiomys* and *P. crinitus*, or convergent events would be required to explain the distribution of chromosomal morphs.

The role of heterochromatin in evolution is poorly understood. The hypothesis that heterochromatin represents "junk DNA" and thus is of no genetic value does not appear likely, based on available data for the genus *Peromyscus*. C-band data for *Baiomys taylori* and *P. alstoni* support the contention of Greenbaum and Baker (1978) that the primitive karyotype for the genus *Peromyscus* contained little heterochromatin. It is thus likely that heterochromatin has been added to the karyotypes of certain species of *Peromyscus* instead of deleted from others. Greenbaum and Baker (1978) showed that heterochromatin had indeed been added to the karyotype of *P. maniculatus*. Another widely distributed species, *P. eremicus*, also shows large amounts of C-band positive material in its karyotype (Greenbaum and Baker, 1978). Our findings that the karyotype of *P. alstoni* (which has a very restricted geographic distribution) contains very little heterochromatin may support the suggestion of Greenbaum and Baker (1978) that heterochromatin increases the amount or release of developmental or phenotypic variation, which would be an important asset to a species occupying a wide variety of habitats. Comparisons of C-banding patterns for a variety of species will be required before the value of heterochromatin can be ascertained.

#### ACKNOWLEDGMENTS

We thank R. A. Bass, Oscar F. Francke, I. F. Greenbaum, R. L. Honeycutt, M. A. Johnson, and Donn E. Rosen for critically reviewing the manu-

script. This study was made possible through a Graduate Student-Faculty research grant from the Graduate School, Texas Tech University, by National Science Foundation grant DEB 76-20580, and the Institute of Museum Research.

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Manuscript received April 1978  
Revised August 1978

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