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KARYOTYPIC VARIATION IN ORYZOMYINE RODENTS (CRICETINAE) WITH COMMENTS ON CHROMOSOMAL EVOLUTION IN THE NEOTROPICAL CRICETINE COMPLEX

By Alfred L. Gardner and James L. Patton

The Neotropical cricetine rodents comprise a highly diversified group of sylvan and pastoral species inhabiting essentially all of South America and tropical and subtropical North America (Hershkovitz, 1962). Included within the tribe Sigmodontini (sensu Hershkovitz, 1966b:747) of the subfamily Cricetinae are over 40 recognized genera. Probably, those that are primarily or exclusively South American in distribution have evolved there via an extensive radiation during the latter half of the Tertiary (Hershkovitz, 1969, 1972, and Savage, 1974; but see Patterson and Fascal, 1968, 1972, and Simpson, 1950, 1969, for alternative opinions). Whatever the place and time span of this radiation, six to eight separate groups have become differentiated. To date they have not been well defined and none are formally recognized at the suprageneric level. Nevertheless, adaptive types spanning the arboreal, subfossorial, and aquatic habits range have emerged, and together they represent one of the most diversified yet obviously closely related assemblages of rodents presently recognized.

Because of the extreme divergence in morphology, systematists generally

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have experienced difficulty in assessing relationships between species as well
as affinities between higher taxonomic categories, and the multiplicity of
named forms has made the identification of many species an extremely ardu-
ous task.

Neotropical cricetines with complex penes include four widespread and
quite diverse groups and five that are somewhat restricted and less diverse
(Hershkovitz, 1962). Included in the former are the akodont, sigmodont,
phyllostine, and oryzomyine rodents; in the latter are the thomomysine,
oxymycterine, scapteromysine, wiedomysine, and ichthyomyine groups. Only
two recent comprehensive revisionary efforts (Pearson, 1958; Hershkovitz,
1962) have been attempted, and both have dealt principally with the phyllo-
tines. Thus, detailed knowledge of species units and their geographic vari-
ation is almost totally lacking for the vast majority of South American forms.
Moreover, knowledge of inter- and intragroup relationships is also meager
and is limited essentially to the information included in the morphological
accounts of Arata (1964), Carleton (1973), Hershkovitz (1944, 1948,

In this paper, we are attempting a clarification of some of the species rela-
tionships within the oryzomyines in addition to summarizing their evolution-
ary trends as indicated by available karyotypic data. Our emphasis has
been on clarifying the kinds and patterns of variation at this level and apply-
ing these interpretations to comparable data for the Sigmoidontini as a unit.

The oryzomyine complex itself comprises a largely sylvan, granivorous
group that has been considered structurally and ecologically close to the stem
stock of the Neotropical cricetines. As presently understood the oryzomyines
include five genera, the three most dominant and widespread of which are
emphasized herein: the rice rats, Oryzomys Baird; the water rats, Neotomys
Peters; and the spiny mice, Neacomys Thomas. Oryzomys includes at least
eight subgenera for which chromosomal data from all but two (Macrorory-
zomys and Micronectomys) are now available. As demonstrated beyond,
these data are indicative of the diversity of forms within the oryzomyine com-
plex and aid in the clarification of phylogenetic units and relationships both
within this group and between the other groups of Neotropical cricetines.

METHODS AND MATERIALS

A total of 164 specimens of oryzomyine rodents of the genera Oryzomys,
Neotomys, and Neacomys were examined for chromosomal characteristics.
In addition, we similarly studied representatives of 14 other genera of Neotropical cricetines for which karyotypes are on file in the following repositories: the Museum of Vertebrate Zoology, University of California, Berkeley; the Museum of Zoology, Louisiana State University, Baton Rouge; or the Division of Mammals, National Museum of Natural History, Washington, D.C. In all cases c-metaphase chromosomes from dividing bone marrow cells were prepared by means of the basic in vivo colchicine-hypotonic citrate sequence described by Patton (1967).

The determination of diploid numbers and chromosome morphology for each animal followed standard procedures (Bender and Chu, 1963; Nadler and Block, 1962). Fundamental number is used herein to designate only the number of autosomal arms. A four-class system for the autosomal complements of each species is used in the descriptions: meta- and submetacentrics, subtelocentrics, and acrocentrics. The definitions of these groupings were given by Patton (1967).

All the karyotyped animals have been prepared as standard museum specimens (skin and skull) and are deposited either in the Museum of Zoology, Louisiana State University (LSUMZ), the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), or the National Museum of Natural History (USNM) as indicated in the species accounts within the karyotypic description section.

KARYOTYPIC DESCRIPTIONS

ORYZOMYS Baird

Subgenus ORYZOMYS Baird

ORYZOMYS albicularis (Tomes).—Kiblisky (1969) has reported on the karyotype of 3 females and 2 males of this species from Rancho Grande, Estado de Aragua, Venezuela. The karyotype of these animals may be described as follows: \(2n=66, \text{FN}=86\); 11 pairs of medium-sized to small meta-submetacentrics and 21 pairs of large to small acrocentric autosomes; a medium-sized metacentric \(X\) chromosome and a small submetacentric \(Y\) chromosome. Colombian and Peruvian material tentatively referred to this species includes three distinctive karyotypic variants:

1. \(2n=66, \text{FN}=112\) (Fig. 1A). Autosomes: 15 pairs of medium-sized to small metacentrics and submetacentrics; 1 pair of large, 4 pairs of medium-sized, and 4 pairs of small subtelocentrics; and 1 pair of large,
FIGURE 1. Representative karyotypes of members of the "albigularis chromosome group" of Oryzomys (s.s.). A) Oryzomys albigularis (Tomes), variant 1; 2n=65, FN=112; female; San Lorenzo, Cerro San Lorenzo, Depto. Magdalena, Colombia; USNM 507238. B) Oryzomys albigularis (Tomes), variant 2; 2n=66, FN=94; male; Peñablanca, Río Pichindé, Depto. Valle, Colombia; USNM 507242. C) Oryzomys albigularis (Tomes), variant 3; 2n=88, FN=92; male; Yuracryaca, Depto. Ayacucho, Perú; LSUMZ 16673. D) Oryzomys auriventer Thomas; 2n=70, FN=84; male; Huambachayo, Depto. Ayacucho, Perú; LSUMZ 16667. E) Oryzomys nigritus (Thomas); 2n=83, FN=86; female; Salta, Río Curanja, Depto. Loreto, Perú; MVZ 136574.

3 pairs of medium-sized, and 4 pairs of small acrocentrics. Sex chromosomes: X, a medium-sized metacentric; Y, a small submetacentric.


(2) 2n=66, FN=94 (Fig. 1B). Autosomes: 9 pairs of medium-sized to small metacentrics and submetacentrics; 3 pairs of large and 3 pairs of
small subtelocentrics; and 1 pair of large and 16 pairs of medium-sized to small acrocentrics. Sex chromosomes: X, a large acrocentric; Y, a small submetacentric.

Specimens examined. COLOMBIA. Depto. Valle: Peñas Blancas, Río Pichindé (2 males, 1 female—USNM 507241-43).

(3) \(2n=80, \text{FN}=92\) (Fig. 1C). Autosomes: 7 pairs of medium-sized to small metacentrics and submetacentrics; 32 pairs of acrocentrics graded from large to small. Sex chromosomes: X, a very large subtelocentric; Y, a small acrocentric.


*Oryzomys auriventer* Thomas.—\(2n=70, \text{FN}=84\) (Fig. 1D). Autosomes: 8 pairs of medium-sized to small metacentrics and submetacentrics; 26 pairs of acrocentrics graded from large to small. If, however, we consider the largest pair of autosomes as subtelocentric, the FN would be 86. Sex chromosomes: X, a medium-sized metacentric; Y, a small submetacentric.

Specimens examined. PERÚ. Depto. Ayacucho: Huanhuachayo (1 male, 2 females—LSUMZ 16667-69).

*Oryzomys nitidus* (Thomas).—\(2n=80, \text{FN}=86\) (Fig. 1E). Autosomes: 4 pairs of small metacentrics; 1 pair of distinctly large acrocentrics and 34 additional pairs graded from large to small. Sex chromosomes: X, a very large subtelocentric; Y, a small acrocentric.

Specimens examined. PERÚ. Depto. Ayacucho: Hda. Luisiana, Río Apurímac (3 males—LSUMZ 16662-63 and 16665); San José, Río Santa Rosa (1 female—LSUMZ 16693). Depto. Loreto: Balta, Río Curanja (5 males, 4 females—LSUMZ 14357, 14365, 16690-91, and 16694; MVZ 136573-74, 136576, and 136578).

*Oryzomys yagouaroundi* Thomas (Fig. 2).—We have recorded two karyotypic variants of this species.

(1) \(2n=60, \text{FN}=66\) (Fig. 2A). Autosomes: 4 pairs of small metacentrics and submetacentrics; 25 pairs of acrocentrics graded from large to small. Sex chromosomes: X, a large acrocentric; Y, presumably a medium-sized or small acrocentric.
Figure 2. Representative karyotypes of members of the "poliurius chromosome group" (A-D) and "komycinus chromosome group" of *Oryzomys* (s.s.). A) *Oryzomys yunguana* Thomas, variant 1; 2n=60, FN=66; female; San José, Río Santa Rosa, Depto. Ayacucho, Perú; LSUMZ 16689. B) *Oryzomys yunguana* Thomas, variant 2; 2n=58, FN=62; male; Balta, Río Curanja, Depto. Loreto, Perú; MVZ 136585. C) *Oryzomys capito* (Olfers); 2n=52, FN=62; male; Balta, Río Curanja, Depto. Loreto, Perú; MVZ 136577. D) *Oryzomys xanthoeolus* Thomas; 2n=56, FN=58; male; 2 mi. W Porculla Pass, Depto. Lambayeque, Perú; MVZ 137943. E) *Oryzomys komycinus* Goldman; 2n=58, FN=80; female; Cariari, Prov. Limón, Costa Rica; LSUMZ 15326.

Specimens examined. Perú: Depto. Ayacucho: San José, Río Santa Rosa (1 male, 2 females—LSUMZ 16685, 16687, and 16689).

(2) 2n=58, FN=62 (Fig. 2B). The karyotype of this form is nearly identical to the one immediately preceding except for the absence of one pair of small metacentric chromosomes.

Oryzomys capito (Olufers).—2n=52, FN=62 (Fig. 2C). Autosomes: 6 pairs of medium-sized to small metacentrics and submetacentrics; 1 very large pair of acrocentrics and 18 additional pairs graded from large to small. Sex chromosomes: X, a large acrocentric; Y, a small acrocentric.

Specimens examined. Peru: Depto. Junín: 3.2 km N Vitoc, Río Tulumayo (1 male—USNM 507246). Depto. Ayacucho: Hda. Luisiana (3 males, 2 females—LSUMZ 16664, 16666, 16677-79); San José, Río Santa Rosa (1 male, 1 female—16686 and 16688). Depto. Loreto: Balta, Río Curanja (10 males, 4 females—LSUMZ 14538, 16680, 16682-83, 16692; MVZ 136575, 136577, 136579-80, 136582-84, 136586, and 136589).

Oryzomys palustris (Harlan).—2n=56, FN=56. Autosomes: 1 pair of small metacentrics; 1 conspicuously large pair of acrocentrics and 23 additional pairs graded from large to small. Sex chromosomes: X, a large acrocentric; Y, a minute acrocentric. A karyotype of this species was presented by Hsu and Benirschke (1969), and our specimens do not differ in any respect.


Oryzomys xanthaeolus Thomas.—2n=56, FN=58 (Fig. 2D). Autosomes: 2 pairs of small meta-submetacentrics; 1 distinctly large pair of acrocentrics and 24 additional pairs graded from large to small. Sex chromosomes: X, a large acrocentric; Y, a small acrocentric.

Specimens examined. Peru: Depto. Lambayeque: 2 mi. W Porculla Pass (1 male—MVZ 137943). Depto. Lima: Lomas de Lachay (1 male, 1 female—USNM 507255-56); Cañete (1 female—LSUMZ 16661); 7 km. SSE Chiksa (1 male, 1 female—MVZ 137592-93).

Oryzomys baarti J. A. Allen.—2n=56; FN=58. The karyotype of this species is essentially identical in all respects to that of O. xanthaeolus (see Fig. 2D).

Specimens examined. Ecuador: Galápagos Islands, Barrington Cove, Isla Santa Fe (=Barrington) (3 males, 3 females—MVZ 145376-81).

Oryzomys bombaycinus Goldman.—2n=58; FN=80 (Fig. 2E). Autosomes: 2 pairs of very small metacentrics; 9 pairs of large to medium-sized metacentrics and submetacentrics; 1 pair of large subtelocentrics; and 16
Figure 3. Representative karyotypes of members of *Oryzomys*, subgenus *Oligoryzomys*. A) *Oryzomys longicaudatus* (Bennett), variant 1; 2n=68, FN=74 or 76; female; 2 mi. E Puquio, Depto. Ayacucho, Perú; MVZ 139219. B) *Oryzomys longicaudatus* (Bennett), variant 2; 2n=64, FN=66; male; Balta, Rio Curanja, Depto. Loreto, Perú; MVZ 136611. C) *Oryzomys longicaudatus* (Bennett), variant 3; 2n=62, FN=74 or 76; female; Bolivar, Venezuela. D) *Oryzomys longicaudatus* (Bennett), variant 4; 2n=60, FN=76; male; Huanchachay, Depto. Ayacucho, Perú; LSUMZ 16697. E) *Oryzomys andinus* Osgood; 2n=60, FN=70; male; 2 mi. W Yupash, Depto. Ancash, Perú; MVZ 139218. F) *Oryzomys fulvescens* (Saussure); 2n=54, FN=68; male; Santa Ana, Prov. San José, Costa Rica; LSUMZ 13169.

Pairs of small acrocentrics. *Sex chromosomes*: X, a large subtelocentric; Y, a small acrocentric.

Specimens examined. **Costa Rica**. Prov. Limón: Cariari (2 males, 3 females—LSUMZ 13171-72, 13174, 13176, and 15326).

*Oryzomys macconnelli* Thomas.—2n=64; FN=64. Unfortunately, the chromosomal preparations from the only specimen examined neither make
the composition of a photo-idiogram advisable nor permit the unequivocal identification of the morphologies of all the chromosomes. Nevertheless, the diploid number is clearly 64 and the karyotype appears to consist of 1 pair of small metacentrics and 31 pairs of acrocentrics graded from large to small. Since it is unlikely that the small metacentrics represent the sex chromosomes, the X and Y are probably acrocentrics and the FN is given as 64.

Specimen examined. PERÚ. Depto. Loreto: Balta, Río Curanja (1 female—LSUMZ 14366).

Subgenus Oligoryzomys Bangs

Oryzomys longicaudatus (Bennett).—Our material referable to this species (sensu lato) includes four distinctive karyotypes, which we describe as follows:

(1) 2n = 68; FN = 74 or 76 (Fig. 3A). Autosomes: 1 pair of large subtelocentrics; 4 pairs of small metacentrics and submetacentrics; and 29 pairs of acrocentrics graded from large to small. The sex chromosomes are not distinguishable since only a female was examined; however, the X chromosomes are most likely the pair of subtelocentrics.

Specimen examined. PERÚ. Depto. Ayacucho: 2 mi. E Pucio (1 female—MVZ 139219).

(2) 2n = 64; FN = 66 (Fig. 3B). Autosomes: 1 pair of large subtelocentrics; 1 pair of small metacentrics; and 29 pairs of medium-sized to small acrocentrics. Sex chromosomes: X, a large subtelocentric; Y, a small acrocentric.


(3) 2n = 62; FN = 74 or 76 (Fig. 3C). Autosomes: 1 pair of large and 4 pairs of small metacentrics; 3 large to small pairs of subtelocentrics; 1 very large and 22 small pairs of acrocentrics. Sex chromosomes: not known since only a female was examined.

Specimen examined. VENEZUELA. Bolívar: (1 female—courtesy of O. A. Reig and P. Kiblisky).
(4) $2n=60$; FN=76 (Fig. 3D). Automes: 2 large and 7 medium-sized to small pairs of metacentrics and submetacentrics; 1 pair of large and 19 pairs of small acrocentrics. Sex chromosomes: X, a large submetacentric; Y, a medium-sized metacentric.

Specimens examined. Perú. Depto. Junín: 3.2 km N Vitoc, Río Tulumayo (1 female—USNM 507224). Depto. Ayacucho: San José, Río Santa Rosa (1 male—LSUMZ 16700); Huancucho (2 males—LSUMZ 16697 and 16701).

Oryzomys aninius Osgood.—$2n=60$; FN=70 (Fig. 3E). Automes: 2 large, 1 medium-sized, and 3 small pairs of metacentrics and submetacentrics; 1 large and 22 small pairs of acrocentrics. Sex chromosomes: X, a large acrocentric; Y, a small acrocentric.


Oryzomys fulvescens (Saussure).—$2n=54$; FN=68 (Fig. 3F). Automes: 1 pair of large and 4 pairs of small metacentrics and submeta-

Figure 4. Representative karyotypes of members of the subgenus Microromys (A) and Melanomys (B), and the genus Oryzomys (C). A) Oryzomys minutus alissinus Osgood; $2n=57$, FN={58}; female; 4 mi. S. 3 mi. E Recuay, Depto. Ancash, Perú; MVZ 137924. B) Oryzomys caliginosus (Tomes); $2n=56$, FN={58}; male; Cariari, Prov. Limón, Costa Rica; LSUMZ 13192. C) Neoromys nadoroughi Heller; $2n=32$, FN=50; male; Punta Espinosa, Isla Fernandina, Galápagos Islands, Ecuador; MVZ 145387.
centrics; 3 pairs of large subtelocentrics; and 18 pairs of small acrocentrics. Sex chromosomes: X, a larger medium-sized acrocentric; Y, a smaller medium-sized acrocentric.

Specimen examined. COSTA RICA. Prov. San José: Santa Ana (1 male—LSUMZ 13169).

Subgenus *Microoryzomys* Thomas

*Oryzomys minutus altissimus* Osgood.—2n = 57; FN = 58 (Fig. 4A). *Autosomes*: 27 pairs of acrocentrics graded from large to small; 3 unpaired chromosomes consisting of 1 large subtelocentric, 1 large acrocentric, and 1 small acrocentric. Sex chromosomes: unknown as only a female was examined.

This individual is apparently a heterozygote for a Robertsonian translocation, as all cells counted (N = 52) possessed an uneven diploid number of 57. A diploid number of 58 has been reported for a male of this species from Venezuela (Kiblisey, 1969:1339).


Subgenus *Mesomys* Thomas

*Oryzomys edgariae* (Tomes).—2n = 56; FN = 58 (Fig. 4B). *Autosomes*: 1 pair of conspicuously large acrocentrics; 24 pairs of medium-sized to small acrocentrics; and 2 pairs of small metacentrics. Sex chromosomes: X, a subtelocentric, the largest chromosome of the entire complement; Y, a medium-sized subtelocentric.


Subgenus *Sigmodontomys* J. A. Allen

*Oryzomys alfari* (J. A. Allen).—2n = 56; FN = 54 (Fig. 6A). *Autosomes*: 27 pairs of acrocentrics grading evenly from large to small. Sex chromosomes: X, a larger medium-sized acrocentric; Y, a small acrocentric.

Figure 5. Representative karyotypes of members of the genus *Oecomys*. A) *Oecomys bicolor* (Tomes); 2n=80, FN=134 or 136; female; Balta, Río Curanja, Depto. Loreto, Perú; MVZ 136592. B) *Oecomys concolor* (Wagner), variant 1; 2n=80, FN=112; male; Balta, Río Curanja, Depto. Loreto, Perú; LSUMZ 16675. C) *Oecomys concolor* (Wagner), variant 2; 2n=60, FN=62; male; Finca Buque, Villavicencio, Intend. Meta, Colombia; USNM 507250.

**Nesoryzomys** Heller

*Nesoryzomys narboroughi* Heller.—2n=32; FN=50 (Fig. 4C). Autosomes: 8 pairs of metacentrics and submetacentrics graded from large to medium-sized; 1 large pair and 1 medium-sized pair of subtelocentrics; and 1 medium-sized pair and 4 small pairs of acrocentrics. Sex chromosomes: X, a medium-sized acrocentric; Y, a small acrocentric.

Specimens examined. **ECUADOR.** Galápagos Islands: Punta Espinosa, Isla Fernandina (=Narborough) (3 males, 3 females—MVZ 145386-91).

**Oecomys** Thomas

*Oecomys bicolor* (Tomes).—2n=80; FN=134 or 136 (Fig. 5A). Autosomes: 1 pair of very large submetacentrics; 22 pairs of medium-sized to small metacentrics and submetacentrics; 1 pair of large and 5 pairs of medium-sized subtelocentrics; and 11 pairs of acrocentrics graded from large to small. Sex chromosomes: unknown since only females have been examined.

Specimens examined. **PERÚ.** Depto. Loreto: Balta, Río Curanja (4 females—MVZ 136592-93; LSUMZ 14362-63).
Oecomys concolor (Wagner).—We have examined chromosomal material from two populations identified as representing this species and each is characterized by a distinctive karyotype:

(1) 2n = 80; FN = 112 (Fig. 5B). **Autosomes**: 1 very large pair of submetacentrics; 11 pairs of medium-sized to small metacentrics and submetacentrics; 1 pair of large and 4 pairs of medium-sized subtelocentrics; and a graded series of 22 pairs of large to small acrocentrics. **Sex chromosomes**: X, a medium-sized submetacentric; Y, a small metacentric.

![Karyotypes](image)

**Figure 6.** Representative karyotypes of members of the genera *Oryzomys* (*Sigmodontomyz*), *Neotomys*, and *Neocomys*. A) *Oryzomys alfar* (J. A. Allen); 2n = 56, FN = 54; male; Pacuare, Río Pacuare, Prov. Cartago, Costa Rica; LSUMZ 13201. B) *Neotomys squamipes* (Brants), variant 1; 2n = 52, FN = 52; male; Yarinacocha, Depto. Loreto, Perú; LSUMZ 14374. C) *Neotomys squamipes* (Brants), variant 2; 2n = 42, FN = 40; male; Balta, Río Caranía, Depto. Loreto, Perú; MVZ 136641. D) *Neotomys squamipes* (Brants), variant 3; 2n = 38, FN = 40; male; Hda. Lusiana, Río Apurímac, Depto. Ayacucho, Perú; LSUMZ 16711. E) *Neocomys spinatus* (Thomas); 2n = 64, FN = 68; male; Balta, Río Caranía, Depto. Loreto, Perú; MVZ 139185.
Specimen examined. **Perú.** Depto. Loreto: Balta, Río Curanja (1 male—LSUMZ 16676).

(2) $2n=60$; $FN=62$ (Fig. 3C). **Autosomes:** 1 pair of small metacentrics; 1 pair of large subtelocentrics; and a graded series of 27 pairs of large to small acrocentrics. **Sex chromosomes:** $X$, a large submetacentric; $Y$, a medium-sized subtelocentric.


**Nectomys** Peters

**Nectomys squamipes** (Brants).—We have examined three karyotypically distinctive populations of this species (sensu lato) and they are described as follows:

(1) $2n=52$; $FN=52$ (Fig. 6B). **Autosomes:** 1 pair of small metacentrics; 24 pairs of acrocentrics sharply divided into 10 pairs of large to medium-sized chromosomes and 14 pairs of small to very small chromosomes. **Sex chromosomes:** $X$, a large medium-sized subtelocentric; $Y$, a smaller medium-sized subtelocentric.

Specimens examined. **Perú.** Depto. Loreto: Yarinacocha (2 males, 2 females—LSUMZ 14371-74).

(2) $2n=42$; $FN=40$ (Fig. 6C). **Autosomes:** 20 pairs of acrocentrics of two size classes—10 pairs of large to medium-sized and 10 pairs of small to very small chromosomes. **Sex chromosomes:** $X$, a medium-sized acrocentric; $Y$, a small acrocentric.

Specimen examined. **Perú.** Depto. Loreto: Balta, Río Curanja (1 male—MVZ 136641).

(3) $2n=38$; $FN=40$ (Fig. 6D). **Autosomes:** 2 very large pairs of submetacentrics; 1 large, 5 medium-sized, and 10 small to very small pairs of acrocentrics. **Sex chromosomes:** $X$, a medium-sized acrocentric; $Y$, a small acrocentric.

Specimens examined. **Perú.** Depto. Junín: 3.2 km. N Vitoc, Río Tulumayo (1 female—USNM 507262). Depto. Ayacucho: Hda. Luisiana, Río Aparimaac (2 males—LSUMZ 16711-12); San José, Río Santa Rosa (1 female—LSUMZ 16715).
Neacomys Thomas

Neacomys spinosus (Thomas).—2n=64; FN=68 (Fig. 6E). Autosomes: 3 pairs of small metacentrics; 1 pair of very large acrocentrics; and a graded series of 27 pairs of large to small acrocentrics. Sex chromosome: X, a large subtelocentric; Y, a small acrocentric.


Karyotypic Affinities

The oryzomyine group of Neotropical cricetines is karyotypically monomorphic. The range in diploid and fundamental numbers (32-80 and 40-136, respectively; see Table 1) is as great or greater than that known for any group of mammals of equivalent taxonomic rank. The exceptional range of variability in both features suggests that karyotypic evolution within the group is exceedingly complex and involves numerous Robertsonian and non-Robertsonian rearrangements.

Extant Neotropical cricetines are surely a product of significantly rapid adaptive radiations following the entrance of the basal stock(s) into South America during mid-Tertiary to late Tertiary times. There is a strong correlation between a wide range in observable karyotypic characters and this mode of evolution. Such a range contrasts with the chromosomal stability and uniformity following adaptive radiation in Hawaiian drosophilids observed by Carson et al. (1967), wherein distinctive taxa were found to be undifferentiated karyotypically. In the case of the oryzomyines and other New World, complex-penis-type Cricetinae, chromosomal reorganization may have played a major causal role in the speciation process during what clearly appears to have been an explosive phase of radiation within the group. This interpretation would support Mares' (1975) projection of a Pliocene colonization of the South American land mass and does not necessitate earlier (pre-Pliocene) arrival of the ancestral sigmodontine stock(s), which has been hypothesized by Hershkovitz (1966b, 1969, and 1972) and Savage (1974). The differentiation of Neotropical cricetine rodents in Middle America prior to their invasion of South America (Patterson and Pascual,
Chromosomal Patterns Within the Oryzomyine Group

In general, the oryzomyine complex is recognizable on chromosomal grounds as a unified group with few obvious deviations from a general plan. Six groupings are evident within the approximately 34 taxa or karyotypic variants examined. Additional material may well fill in the apparent gaps between some of these assemblages; nevertheless, the diversity of the forms we have examined is sufficient to prove the utility of karyotypic data in identifying taxonomic units and in elucidating cricetine relationships.

Perhaps the most comprehensive group includes *O. palaeiris*, *O. yunganus* (chromosomal variants 1 and 2), *O. capito*, *O. xanthacolus*, *O. bauri*, and *O. macconnelli* of the nominate subgenus, along with *O. (Melanomys) caliginosus*, and *O. (Microryzomyys) minusculus*. These species are characterized by moderately high diploid numbers (52-64), moderately high fundamental numbers (52-68), and an essentially evenly gradated, basically acrocentric autosomal complement containing six or fewer pairs of small biarmed elements. Their sex chromosomes are similar in size and morphology except for those of *O. (Melanomys) caliginosus*, which possess unique X and Y elements (see Fig. 4B). *Oryzomys yunganus*, *O. macconnelli*, and often *O. nitidus* (chromosomally grouped with *O. albicans*) are usually treated as synonyms of *O. capito*. Chromosomal and morphological features, however, verify their validity as full species. We collected *O. yunganus* and *O. nitidus* together with *O. capito* at San José, Depto. Ayacucho, Perú and all three in the same traps with *O. macconnelli* at Balta, Depto. Loreto, Perú. *Oryzomys bauri* and *O. xanthacolus* are obviously closely related. Indeed, the mainland *O. xanthacolus* is the most logical ancestor of the Galápagos *O. bauri* and *O. galapagoensis* on chromosomal as well as on morphological grounds.

*Neotomys (Sigmodontomys) alfari* (Fig. 6A) is very closely allied chromosomally with this group—a fact that supports the inclusion of this species within the genus *Oryzomys*, as suggested by Hooper and Musser (1964) on the basis of phallic morphology. As was pointed out by Hershkovitz (1966a:136), however, the glans penis of *Neotomys* (sensu stricto) had not yet been described and, hence, the apparent similarity of *N. (Sigmodontomys) alfari* with species of *Oryzomys* could not be fully evaluated. We
have recently examined prepared glanes from three specimens of *Nectomys* (s.s.) *squamipes*, chromosomal variant 2 (Fig. 7). The baculum is short and massive with an extremely broad base that bears a proximal notch; and the bacular mound is enlarged and robust with the lateral digits longer, better developed, and projecting somewhat more ventrally than the medial digit. The overall external aspect of the glans is decidedly oryzomyine in appearance. Nevertheless, the glans and baculum of *N. squamipes* shows little resemblance to the penis of *N. (Sigmodontomys) alfaroi* or to that of any *Oryzomys* of which we are aware. Thus, the subgenus *Sigmodontomys* is no more differentiated cytologically or in penis morphology from *Oryzomys* than is *Melanomys*, for example; and all evidence places it closer to *Oryzomys* than to *Nectomys*. For these reasons we are treating *Sigmodontomys* as a subgenus of *Oryzomys*.

The otherwise distinctive *Neacomys spinosus* (Fig. 6E) is chromosomally differentiated only slightly from this group in possessing a higher fundamental number (68). The Colombian and Peruvian populations of *N. spinosus* we have sampled are karyotypically identical.

*Oryzomys bombycinus* (Fig. 2E) with its high number of large, biarmed autosomes and high fundamental number (80) is one of the most strongly differentiated members of the subgenus *Oryzomys*. Its relationship with other members of this subgenus is obscure. Perhaps *O. bombycinus* has closer affinities with *O. melanotis* and the "O. alfaroi group" as suggested by Hershkovitz (1966b:736). Karyotypic data from either of the latter are currently lacking.

A third oryzomyine group is comprised of *O. nitidus, O. auriventer*, and the karyotypic variants of *O. albivularis* (sensu lato), all characterized by high diploid and fundamental numbers (66-80 and 84-112, respectively). There are two basic karyotypes based on diploid number among the mice we have identified as *O. albivularis*. The Peruvian populations are distinguished by a diploid number of 80 and a principally acrocentric autosomal complement. The Colombian populations we have sampled and the Venezuelan animals Kiblisky (1969) reported on all have a diploid number of 66 with greater numbers of biarmed autosomes (11 to 24 pairs as opposed to 7 pairs in the Peruvian populations). We believe that the different diploid numbers represent different species. However, additional populations must be analyzed, particularly the population represented by the holotype of *O. albivularis* (from Pallatanga, Ecuador), before the rela-
tionships can be resolved. Of the 66-chromosome forms, the Colombian population from Peñas Blancas and the Venezuelan population from Rancho Grande are closer karyotypically than either is to the geographically intermediate San Lorenzo population. The karyotype of the Peñas Blancas O. albignarlis differs from that of the Rancho Grande form in having four more pairs of biarmed autosomes, four fewer pairs of unarm ed elements, and a large acrocentric instead of a medium-sized metacentric X chromosome. Pericentric inversions or heterochromatin additions or deletions could account for the autosomal karyotypic differences, including that of fundamental number. Presumably, the karyotype characterizing the San Lorenzo population, with its unusually high fundamental number (112), is a reflection of the isolated location of the Cerro de San Lorenzo (part of the Sierra de Santa Marta) and the geographic separation of this range from the northern extreme of the eastern Andes. As those elsewhere, these O. albignarls are forest inhabitants occurring at middle to upper elevations. The only karyotypic similarities held in common with the Venezuelan O.

Figure 7. The glans penis of Nectomys squamipes, Baíta, Río Curanja, Depto. Loreto, Perú; MVZ 136691: a, ventral view; b, lateral view.
*Oryzomys nitidus*, while very similar karyotypically to the *albigularis*-group, where we have placed it for the purpose of this discussion, is not closely related to either *O. auriventer* or *O. albigularis* (sensu lato). The karyotype of *O. nitidus* (Fig. 1E) is closest to that of the Peruvian *O. albigularis* (*2n* = 80, FN = 92), differing from the latter only in possessing three fewer pairs of small meta- and submetacentric autosomes. Dental and cranial characters, however, do not indicate a particularly close taxonomic relationship. Originally described by Thomas (1884:452) as a reddish variant of *Hesperomys laticeps* (= *O. capito*), *O. nitidus* is found in tropical forest habitats at low elevations and, in our experience, sympatric with *O. yungaicus*, *O. macconnelli*, and particularly *O. capito* (a species with which it is commonly confused). Hershkovitz (1966a:138) considered *O. nitidus* as representing *O. alfaroii* (a species we have not examined) and distinct from *O. capito*.

Several investigators (e.g. Cabrera, 1961; Hooper and Musser, 1964: 46) have directly or indirectly recommended abandoning the subgenus *Oligoryzomys* because, in their opinion, it is, at best, only weakly differentiated from *Oryzomys* (sensu stricto). We disagree, however, since *Oligoryzomys*, next to *Oecomys*, and *Neoryzomys*, chromosomally represents the most clearly defined affiliation of species within the genus *Oryzomys*. All are characterized by moderately high diploid and fundamental numbers (54–68 and 66–76, respectively) with an autosomal complement that includes one or more pairs of large biarmed and a pair of distinctly large acrocentric or subtelocentric chromosomes, and with most or all of the remaining acrocentric complement comprised of uniformly small to very small elements. The four forms we have described as karyotypic variants of *O. longicaudatus* are well differentiated chromosomally and may each represent a distinct species. We lack the necessary samples to enable us to morphologically characterize each form and, thereby, determine their identities. Hershkovitz has either referred
all *Oligoryzomys* to *Oryzomys nigripes* (1966a:136) or has grouped them as separate species within the *Oryzomys nigripes* complex (1966b:738) with *longicaudatus* a synonym of *nigripes*. We do not know whether one or more of the chromosomal variants of *O. longicaudatus* actually represents *O. nigripes*; therefore, we have chosen to include them under the name *longicaudatus*, a name long used for at least some of the represented populations.

The arboreal rice rats (*Oecomys*) and the endemic Galápagos rats (*Nesoryzomys*) are the most strongly differentiated chromosomally of all of the oryzomyine rodents. Each is at an opposite end of the spectrum of chromosomal variability characterizing the oryzomyine complex, and they show no relationship whatsoever to each other. Among *Oecomys* we have sampled one population of *O. bicolor* and two very distinct populations of *O. concolor*. The eastern Peruvian (Balta) populations of *O. bicolor* and *O. concolor* are characterized by high diploid numbers (80) and very high fundamental numbers (112 to 134 or 136). Were it not for the Colombian *O. concolor* (2n=60, FN=62), there would be no suggestion of relationship between *Oecomys* and any of the species of *Oryzomys*. The Colombian *O. concolor* is karyotypically like the first chromosomal group of *Oryzomys* (sensu stricto) discussed above and, in addition to being annectent between *Oecomys* and the genus *Oryzomys*, clearly points out the composite nature of *Oecomys concolor* (sensu Hershkovitz, 1960). We interpret the Colombian *O. concolor* karyotype as representing chromosomal variation independent of that characterizing *Oryzomys* (sensu stricto) and, despite some structural evidence to the contrary (i.e., phallic morphology—Hooper and Musser, 1964), consider *Oecomys* as a distinct taxon that warrants recognition at the generic level.

We also recommend generic status for *Nesoryzomys*, which represents the sixth oryzomyine chromosomal unit. The karyotypically and structurally distinctive *N. nabaronghi* (Fig. 4C) has the lowest diploid number (32) and, next to the chromosomal variants 2 and 3 of *Neotoma squamipes*, the lowest fundamental number (50) of any member of the oryzomyine complex. *Nesoryzomys* is so aberrant chromosomally as to demand recognition as a full genus. This opinion is supported by several other lines of evidence (see Niethammer, 1964; Patton and Myers, MS).

The remaining oryzomyine rodents we have examined chromosomally
include three chromosomal variants of *Nectomys squamipes* from Perú. The Balta (variant 2) and Hda. Luisiana, San José, and Vitoc (variant 3) populations are readily distinguishable by their low diploid and fundamental numbers. The two karyotypic forms they represent differ by only two centric fusions (see Figs. 6C and D). The Yarinacocha *N. squamipes* (chromosomal variant 1) are superficially similar to the species we grouped with *Oryzomys palustris*, but the distinct division of the acrocentric autosomes into two size classes clearly aligns them with the other *Nectomys*, despite their higher diploid and fundamental numbers and unique sex chromosomes. We believe that the relationship between variant 1 on the one hand and variants 2 and 3 on the other is distant and that more than one species is represented.

**Chromosomal Patterns within the Neotropical Cricetine Complex**

*Composition of suprageneric groupings.*—Karyotypic data are now available from eight of the nine suprageneric groups of complex-penis-type Neotropical cricetines. While a great many gaps still exist in the overall coverage of these groups, the information at hand demonstrates an exceedingly broad range in the basic karyotypic characteristics. Analysis of these data has revealed many discernible chromosomal patterns.

Published information is largely confined to three groups: the akodonts (Bianchi et al., 1971), sigmodonts (Zimmerman, 1970), and phyllotines (Pearson, 1972; Pearson and Patton, in press). With these exceptions and the content of this paper, most of the information on Neotropical cricetines is fragmentary. The available karyotypic data for the nonoryzomyine cricetines included in this report are summarized in Table 2 and outlined in graphic form in Figures 8 and 9.

The phyllotines are the best known group of South American cricetines and were the subject of two recent and extensive revisionary reports (Pearson, 1958; Hershkovitz, 1962). These mice are also the most completely known karyotypically (Pearson, 1972; Pearson and Patton, in press). The phyllotine group is chromosomally miform with diploid and fundamental numbers ranging from 22 to 70 and 30 to 76, respectively.

Pearson and Patton (in press) included these taxa within the phyllotines: the monotypic genera *Andinomys*, *Chinchillula*, *Higmodontia*, *Nectomys*, and *Reithrodon*; and the closely related polytypic *Phyllothris*, *Graomys*, and *Aulis-
Figure 8. Summary of distribution of diploid numbers for taxa representing eight of the nine recognized suprageneric groups of Neotropical cricetines. Data taken from Tables 1 and 2.
Figure 9. Bivariate plot of fundamental number and diploid number for each of the chromosomally known taxa of Neotropical cricetines. Solid lines delimit maximum and minimum values for fundamental numbers possible at any given diploid number.
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comys. The inclusion of Neotomys and Reithrodont (members of the sigmodont group, sensu Hershkovitz, 1962) within the phyllotines was principally based on shared karyotypic features. In addition—particularly for Reithrodont—external, cranial, and dental similarities were taken into consideration. We both concur with this arrangement except possibly with regard to the placement of Neotomys (see beyond). Zygodontomys, on the basis of its high diploid numbers (see Table 2), was excluded by Pearson and Patton from the phyllotine group. Instead, they suggested that its affinities lie closer to the akodonts. We also believe that Zygodontomys is either closely aligned with the akodonts or may comprise a separate group of its own. Comparative phallic morphology led Hooper and Musser (1964) to a similar conclusion. Zygodontomys latiusculus, however, with a diploid number of 34 (Yonenaga, 1973), is sharply distinct karyotypically from the other Zygodontomys and perhaps is best considered as a member of the genus Akodon (sensu lato).

The ichthyomyine group is represented in our material by a female Anotomys leuconotus. The karyotype is distinctive in its high diploid number, the highest yet known for any mammal (Gardner, 1971; see Table 2). Unfortunately, little else can be said regarding this group other than to emphasize its uniqueness and apparent distant relationship to other Sigmodontini. The derivation of this karyotype must have involved a number of centric fissions or other chromosomal rearrangement mechanisms promoting higher diploid numbers.

Akodonts, particularly Argentinian and Venezuelan species, were reviewed recently by Bianchi et al. (1971). Their data, plus those from other sources, are listed in Table 2 and plotted in Figures 8 and 9. While the akodont karyotypes cover a wide range in diploid numbers (14 to 52, not including Zygodontomys) and fundamental numbers (29 to 56), the majority fall within a group characterized by moderate to low diploid and fundamental numbers (2n = 34 to 44, FN = 38 to 48) with predominantly acrocentric autosomal complements. Grossly similar diploid and fundamental numbers are found in other Neotropical cricetines, namely Neotomys squamipes (variants 2 and 3) of the oryzomyine complex, Graomys and Calomys of the phyllotines, and most of the thomazomyines.

Bianchi et al. (1971:724) cite Oswaldo Reig as recommending full generic recognition for Abrothrix, Akodon, Blarinomys, Bolomys, Chroomys, Hystrimys, Lenoxus, Microxus, Notiomys, Oxymycterus, Podomyrys, Talpomys,
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<td>?</td>
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</table>

*oxymycterine group*

| Oxymycteria rutilans  | 54 | 64 | SM | A  | Gentile de Fronza, 1970b       |
| Abrothrix longipilis  | 52 | 54 | ST | A  | Bianchi et al., 1971           |
| Abrothrix xanthobrinus| 52 | 54 | ST | A  | "                              |

*sigmodon group*

<p>| Sigmodon leucotis     | 52 | 52 | A  | A  | &quot;                              |
| Sigmodon alleni       | 52 | 64 | ST | SM | &quot;                              |
| Sigmodon ochrogaster  | 52 | 66 | ST | ST | &quot;                              |</p>
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<th>Species</th>
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<th>N2</th>
<th>Chromosome morphology</th>
<th>A1</th>
<th>A2</th>
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<td>34</td>
<td>A</td>
<td>A</td>
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<td>Hsu and Benirschke, 1969; Lee and Zimmerman, 1969</td>
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<td>28</td>
<td>A</td>
<td>A</td>
<td></td>
<td>Zimmerman, 1970</td>
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<td>56</td>
<td>56</td>
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<td>A</td>
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<td>A</td>
<td>M</td>
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<td>60</td>
<td>SM</td>
<td>A</td>
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<td>Paraguay: Depto. Cordillera (MVZ)</td>
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1 Chromosome morphology described by Patton, 1967.
2 Provenance and deposition given for material first reported herein.
and Thaptomys—taxa that they included within their akodont group of genera. We have followed Hershkovitz (1966a:127) in treating Abrothrix as a member of a separate group, the oxymycterines. The akodont group karyotypes (except for Bolomys altiventer) have all been published as representing species of Akodon. Therefore, we have listed them in this manner in Table 2. The variation in chromosomal characters within some of the Akodon "species" evident in Table 2 demonstrates the lack of unanimity among the various authors regarding the taxonomic identity of their material.

The oxymycterine group includes Oxymycterus, Podoxomys, Lenoxus, and Abrothrix (Microxus is a synonym according to Hershkovitz, 1966a:86). The only karyotype information we have is that reported for Oxymycterus rutilans by Gentile de Fronza (1970b) and for Abrothrix longipilis and A. xantobrhinus by Bianchi et al. (1971). The latter two species have identical karyotypes (Table 2) and all three have chromosomal configurations that are similar in many respects to the broadly based group (2n = 52 to 64, FN = 54 to 68) typified by Oxymycterus palustris and encompassing species belonging to every suprageneric group except the scapteromyines and ichthyomyines.

Our chromosomal information for the scapteromyine group is that reported by Gentile de Fronza (1970a) for Scapteromys aquaticus and by Brum (1965) and Brum et al. (1973) for Scapteromys tomentosus and S. tumidus. Gentile de Fronza (1970a) reported a diploid number of 32 and a fundamental number of 44 (which includes the sex chromosomes) for S. aquaticus. By our definition, the fundamental number of S. aquaticus is 40. Brum (1965:316) reported a diploid number of 24 and fundamental number of 34 for S. tomentosus; but an examination of his figures (p. 318) reveals a fundamental number of 40. These values are the same as those given by Brum et al. (1973) for S. tumidus (2n = 24, FN = 40). Therefore, from the scanty evidence at hand, scapteromyines appear to have low diploid numbers and relatively high fundamental numbers. They are karyotypically similar to Akodon orophilus and Sigmodon arizonae (see Fig. 9) and, in a broader sense, to some other akodonts, sigmodonts, and phyllostines (Glaucomys). We remark on this association without implying any particularly close phyletic affinity. But, since Scapteromys is karyotypically unlike any otronyomyine, thomomysine, or oxymycterine, its relationship may well be closest to either the akodont or sigmodont group (probably the latter).

The sigmodont group (sensu Hershkovitz, 1955:639) includes Sigmodon, Holochilus, Neotomys, and Reithrodon. The "natural" character of this
assemblage has been challenged by Hooper (1952) and Hooper and Musser (1964) on the basis of phallic structure and by Pearson and Patton (in press) on chromosomal grounds. Hooper and Musser claim that Reithrodont is closest to the phyllotines, Holochilus is closest to the oryzyomyines, and both are distinct from Sigmodon (and Sigmodonts). Pearson and Patton reached the same conclusion regarding Reithrodont, and placed it near Aulisconys. They also included Neotomys within the phyllotines, stressing its chromosomal similarities with Phyllostis osilae as well as its chromosomal distinctness from the karyotypically known sigmodonts. The phallus of Neotomys is as yet undescribed.

Brum (1965:315) reported the fundamental number for Reithrodont physodes as 30, a count that includes autosomes and sex chromosomes. We list a fundamental number of 26 (Table 2), the number of autosomal arms evident from Brum’s figure on page 318. Karyotypically, Reithrodont physodes is also similar to Sigmodon mexicanus as well as Aulisconys, differing from the former primarily in the morphology of the X chromosome. Therefore, Reithrodont cannot be assigned to either the phyllotine or sigmodont groups unequivocably on the basis of comparative karyology. For other morphologic and zoogeographic reasons, however, we believe that the karyotypic similarities between Reithrodont and some species of Sigmodont are convergent and that its relationships are with the phyllotines.

Our material of Holochilus brasiliensis includes three distinctive karyotypic variants, respectively representing a northern, central, and southern part of the geographic range of the species. These variants are sufficiently distinctive to suggest that Holochilus brasiliensis of Hershkovitz (1955) is composite. Nevertheless, the Holochilus karyotypes neither support nor deny the close affinity with oryzyomyines suggested by Hooper and Musser (1964). Indeed, the Peruvian specimens are nearly identical chromosomally to several species of both Oryzomyis and Sigmodonts. The differences in cranial and dental structures, however, would seem to refute any close relationship with the oryzyomyine group.

The chromosomal and morphological evidence at hand supports the hypothesis that Neotomys and Reithrodont are phyllotines. The suite of characters linking Neotomys and Reithrodont to the phyllotines would appear to override the significance of their similarities with Sigmodont and Holochilus. Nevertheless, we place Neotomys close to the phylogenetic line leading to the sigmodonts (Fig. 10b) because some features held in common with Sig-
modon indicate that it could be annectent between the phyllotines and the sigmodonts.

The thomasonyine group (sensu Hershkovitz, 1966a:125) includes Thomasonys, Rhipidomys, Nyctomys, Otosomatys, and Phaeomys. Members of this group represented by our material (Table 2) include Rhipidomys latimanus and at least six species of Thomasonys (sensu lato). Aepomys (=Thomasonys) fuscatus (2n=54, FN=62) is karyotypically the most aberrant representative and actually may not belong in the Rhipidomys and Thomasonys complex. Therefore, we are using the generic name Aepomys for this form. Chromosomally it falls within the first oryzomyine group as exemplified by Oryzomys palustris, a group sharing chromosomal characters with various other groups (see Table 2 and Fig. 8).

The remaining thomasonyine species comprise a uniform assemblage characterized by a diploid number of 42 or 44 and a predominantly all acrocentric autosomal complement. Thomasonys monochromus has a diploid number of 42, one pair of very small metacentric autosomes, and submetacentric X chromosomes (the latter being the largest elements in the complement). Otherwise, the thomasonyines we have examined all have 44 chromosomes, three or fewer pairs of biarmed autosomes, and either submetacentric or acrocentric sex chromosomes. We found completely acrocentric karyotypes in T. aureus. Excluding Aepomys fuscatus, the thomasonyines examined, together with some akodonts (at least 13 forms), oryzomyines (Nectomys squamipes, variants 2 and 3), and phyllotines (two species of Calomys and one species of Graomys) form a chromosomal assemblage that is distinguishable by a low diploid number (34 to 44) and low fundamental number (38-48).

Patterns of chromosomal evolution.—The major trends in chromosomal evolution within and between the Neotropical cricetine lineages are summarized in Figure 9, a bivariate plot of fundamental number versus diploid number. A graphic representation of these two variables clearly portrays the pattern of directional change in the autosomal complements within any one group. Lineages in which only Robertsonian types of rearrangements have been utilized (i.e., changes in 2n but not FN brought about by centric fusions or fissions, whole-arm translocations, or other similar mechanisms) will show horizontal linear alignment; those which have proceeded exclusively by non-Robertsonian changes (i.e., changes in FN but not 2n produced by pericentric inversions, various unequal translocations, or whole-arm heterocho-
matin additions or deletions) will be arranged in a vertical linear fashion. Those lineages combining various proportions of both broad groups of mechanisms will be arranged in the diagonal. Diagonally directed groupings can also be the product of other rearrangement mechanisms, which do not fit clearly into either the Robertsonian or non-Robertsonian categories (e.g., tandem fusions).

It is abundantly evident from Figure 9 that in only very few cases do either Robertsonian or non-Robertsonian changes exclusively, or nearly so, characterize the karyotypic evolution in particular lineages of Neotropical cricetines. Below the generic level, the mechanisms of the former group characterize only some phyllotines [e.g., Phyllostis, Anisomys, and Graomys] and those of the latter (non-Robertsonian) characterize only Thomasomys and Rhipidomys. Indeed, the Neotropical cricetines exhibit a very narrow range of observed 2n-FN combinations among taxa examined, although, theoretically the degree of scatter might be many times greater. This narrow range and the observed relationship between diploid and fundamental numbers, which is near unity (slope = 1.07, see Fig. 9), emphasize the equal importance of both Robertsonian and non-Robertsonian mechanisms (or, alternatively, tandem fusions) in the broad-scale evolutionary changes within these lineages. Determinations of the relative proportions of those various mechanisms that have actually been in operation must await more refined cytological analyses (e.g., G- and C-banding) than we can provide here. However, the data suggest that tandem fusions have perhaps played the single most significant role. Although this rearrangement type is considered relatively uncommon, it has clearly been implicated in muroid chromosomal evolution by G-band studies (Mascarello et al., 1974). We believe this mechanism to be important here since nearly all suprageneric groups contain one to many members that have the same karyotypic pattern, which is a basically acrocentric autosomal complement even though diploid numbers may range from the low 40s to 80 or above. If these forms do indeed share a common ancestry, tandem fusions are the most parsimonious rearrangement mechanisms that shift diploid numbers but keep a constant karyotypic pattern intact.

We assume that both increases and decreases in diploid number as well as in fundamental number have occurred during the karyotypic differentiation of the Neotropical cricetines (surely Anisomys leander with 2n=92 must have been derived by fissioning or a similar process). Yet, the apparent general trend is towards a decrease in both 2n and FN. The structurally
FIGURE 10. (concluded). Directional trends and suggested relationships among the Neotropical cricetines based primarily on karyotypic data, but also including an appreciation for cranial, dental, and phallic morphologic characters and zoogeographic considerations.
more primitive groups (e.g., oryzomyines) have higher modal values of diploid and fundamental number than do more advanced groups (e.g., sigmodonts, akodonts, or phyllostines). Furthermore, specialists on the akodonts or phyllostines have presented evidence of a reductional trend in the chromosomal evolution of those groups (Bianchi et al., 1971; Pearson and Patton, in press). Within any given lineage, therefore, the more primitive karyotypes appear to be those with higher diploid numbers, and the more derived to be those with lower numbers. Under the assumption that one result of progressive reduction in chromosome number is the tightening of linkage groups and the concomitant reduction of total recombinatory potential, such derived karyotypes can also be considered evolutionarily cannalized or specialized. Conversely, the ancestral, high-numbered karyotypes can be equated with evolutionary primitiveness. On these bases, the species of *Phyllostis* and *Oryzomys* (s.s.) with respective karyotypes of \(2n=38\), \(FN=72\) and \(2n=52\), \(FN=62\) can be considered more recently derived and further specialized than their congers with respective karyotypes of \(2n=68\), \(FN=70\) and \(2n=80\), \(FN=86\). The logical extension of this line of argument is to conclude that karyotypes of such taxa as *Akodon arviculoides*, *Akodon urichi*, *Sigmodon arizone*, *Auliscomys boliviensis*, *Scapteromys tomentosus*, *Scapteromys tumidus*, and *Reinbroden phylodes* represent the most specialized yet known among the Neotropical cirectine assemblage.

The graph summarizing diploid and fundamental numbers (Fig. 9) also illustrates that the majority of the karyotypes fall significantly close to the lower limit of fundamental numbers possible for any given diploid number (potential FN range indicated by solid diagonal lines). We have interpreted the tendency implied by these data to be toward retention of the chromosomal rearrangement plasticity presumed to be characteristic of low FN/2n ratios. Only *Scapteromys*, *Graomys donorum*, *Calomys lepidus*, *Sigmodon arizone*, *Akodon urichi*, and the six \(2n=38\), \(FN=72\) species of *Phyllostis* have achieved the derived and highly specialized karyotypic state of totally biarmed autosomal complements (high FN/2n ratios). This condition is approached by *Nesoryzomys narbonorghi*, *Akodon orophilus*, and *Auliscomys boliviensis*. The evolutionary cost of these seemingly more stable, derived karyotypes may be a significant reduction in the speciation potential that the possibility of relatively simple chromosomal rearrangements (e.g., Robertsonian fusions) provides.

*Phylogenetic relationships of Neotropical cirectines.*—A summary of the
directional changes in diploid number and our interpretations of phylogenetic relationships among the Neotropical cricetines is presented in Figure 10. The oryzomyine group is considered by us to be the stem stock from which all other lineages were derived. This complex includes a broad array of adaptive types. Most members have generalized scansorial habits, but some have developed toward the totally arboreal habitus (e.g., *Octonyx*) and others are slightly to moderately modified for aquatic existence (e.g., *Neotonyx*). This group also displays a wide range of karyotypic states although most taxa fall within a diploid range of 50 to 80, which by our definition indicates both ancestral and unspecialized karyotypic states. We consider the 70- to 80-chromosome karyotypes of *Oryzomyx* (sensu stricto) to be the most likely progenitor states from which all other Neotropical cricetine lineages were eventually derived. The phylogenetic relationships shown are only gross approximations. While they are based primarily on the karyotypic data summarized above, other features of morphology or zoogeography have tempered the decisions made as to individual generic placement. By treating Zygodontomys as a member of the akodont group, we mean that Zygodontomys and *Akodon* must have shared a common ancestor subsequent to the divergence of that line from somewhere within the oryzomyine complex. If, however, we had placed Zygodontomys in a group of its own, the remaining akodonts would most likely be depicted with closer ties to the phyllostines or sigmodonts than are shown in Figure 10. The phyllostine genera are arranged as in Pearson and Patton (in press), but note that Neotonyx is shown as ancestral to the sigmodonts and could, therefore, be placed in that group.

**Remarks on Taxonomy and Distribution**

That the taxonomic identities of many of the chromosomal forms described or discussed herein are in a muddled state became apparent early in our study. Therefore, we took advantage of opportunities to directly compare representative specimens of known karyotype with holotypes housed in the American Museum of Natural History, the British Museum (Natural History), the Museum of Comparative Zoology at Harvard, and the National Museum of Natural History. A detailed comparative analysis of these specimens, however, is not possible at this time. Instead, we present the following information to explain some of the taxonomic determinations used in this report as well as to update distributional information on certain species and to offer additional data on some of the localities mentioned herein.
Clearly, *Oryzomys albicularis* (sensu Cabrera, 1961:380-383; Hershkovitz, 1944:72, footnote; 1966a:137, footnote) is composite. We have directly compared representative specimens of known karyotype with the holotypes of all of the named forms Cabrera and Hershkovitz considered specific synonyms of *O. albicularis*. With the exception of *O. albicularis boliviae* (see Cabrera, 1961), which we consider equivalent to *O. nitidus*, and *O. villosus* (see Hershkovitz, 1966a:137, footnote), which we believe most closely resembles *O. capito*, *O. albicularis* (sensu lato) is an assemblage of closely related species of large, terrestrial rodents inhabiting humid forests at middle to upper elevations. Most have variable amounts of white on the venter. Usually the white is restricted to the throat, but it may cover the entire ventral surface (e.g., in some *macniventris*). All have relatively large, robust skulls, usually with broad incisive foramina and moderately developed supraorbital ridges. The second upper molars lack an enamel island separating the first primary fold and the major fold (first internal fold coalesced with first primary fold).

Chromosomal and morphological evidence confirms *O. aniventer* as a full species distinct from *O. albicularis*. Our Huanchaco specimens are nearly identical with the holotype. *Oryzomys aniventer nimbosus* is also similar, but markedly smaller. *Oryzomys aniventer* is closest chromosomally to the 2n=66 *O. albicularis* from Colombia and Venezuela, with which it also shares a white patch on the throat.

Chromosomal data have demonstrated at least two species among the remaining named forms of *O. albicularis* (sensu lato). One, represented by Venezuelan and Colombian populations, has 66 chromosomes. The other, represented by two Peruvian populations, has 80 chromosomes. The assignment of either diploid type to *O. albicularis* must await karyotypic information from topotypical material. The type locality of *O. albicularis* (Pallastanga, Ecuador) is geographically between the sources of the 2n=66 and the 2n=80 populations. The Peruvian animals lack white on the venter and most closely resemble *O. keayi*. Therefore, we suspect that the name *albicularis* will prove to be applicable to the 66-chromosome forms.

Hershkovitz synonymized the majority of the named forms of medium-sized terrestrial South American *Oryzomys*, first under *O. laticeps* (1960:544, footnote) and later under *O. capito* (1966a:137, footnote) because he concluded that *capito* had priority. We differ with Hershkovitz in recognizing at least four species among those named forms he specifically listed as
synonyms. Our determinations are based upon direct comparisons of specimens of known karyotype with most of the holotypes that have been available to us. Nevertheless, since we have not examined topotypical examples of capito, our use of that specific epithet is tentative.

The $2n=52$, FN=62 mice we are calling O. capito are characterized as follows: dorsal adult coloration usually buffy brown to yellowish brown (but rufous in some individuals), usually with a broad, darker, mid-dorsal stripe, and with gradation to paler and grayer laterally (immatures dark gray-brown dorsally); ears clothed externally with dark brown hairs and internally with a mixture of whitish and dark brown hairs; incisive foramina comparatively short, broad, and teardrop-shaped; sphenopalatine pits simple; bony excrescences (palatal bridge) usually present on palate; enamel island lacking in the second upper molars (first primary fold coalesced with first internal fold).

Our O. capito are nearly identical with the holotypes of O. goeldi and O. perakensis. Other probable specific synonyms are carrikeri, castaneus, magdalena, medius, modestus, mollipilosus, onicus, talamancae, and velatimis.

The $2n=80$, FN=86 animals from Perú are morphologically identical with the holotype of O. nitidus; consequently, we are using this name for this species. The external features Thomas (1884:453) used to describe nitidus broadly apply to our O. nitidus. Pine (1971:591), after he examined part of Thomas’ series (but not the holotype), remarked, “The external characters Thomas used to distinguish ‘nitidus’ from typical ‘laticeps’ seem reversed. . . .” Thomas’ series was composite, however, and the portion Pine saw apparently did not include true O. nitidus. We have not seen the holotype of O. laticeps and do not know whether this name would be correctly applied to the mice we are calling O. nitidus or is a synonym of O. capito.

Oryzomys nitidus exhibits these characters: dorsal adult coloration reddish brown, grading on the sides to cinnamon along the lateral line (immatures a mixture of gray and reddish brown dorsally); ears clothed internally and externally with black hairs; incisive foramina comparatively long and narrow; sphenopalatine pits usually simple; palatal excrescences (incipient palatal bridge) present in most individuals; enamel island present in the second upper molars between the medial portion of the first primary fold from the major fold (first internal fold discrete).
Specific synonyms of *O. nitidus* include *boliviae* and *legatus*. The cheek teeth of the holotype of *bolivari*s are too worn to show diagnostic features, but otherwise it is the same as our *O. nitidus*. Although we have not seen the holotype of *O. intermedius* (Leche) 1886, the holotype (BM 89. 5. 20. 1) is also like *O. nitidus*; therefore, *bolivari*s and *intermedius* may be synonyms as well.

We have identified the 2n = 64, FN = 64, long-haired, reddish *Oryzomys* from eastern Perú as *O. macconnelli*. It is the first of the species to be recorded from that country. This species is characterized as follows: long and lax, dark reddish brown dorsal pelage; large incisive foramina, widest in the middle and tapering anteriorly and posteriorly; palatal excrescences obsolete; sphenopalatine pits compound; cheek teeth comparatively simple; second upper molars with short first and second primary folds, and with a shallow enamel island between the first primary and major folds (first internal fold discrete, but lost early in wear); and third upper molars with persistent first internal fold and comparatively well-developed major fold. In many respects, *O. macconnelli* resembles members of the *O. albignularis*-complex.

Another species we have distinguished within the "capito-complex" is the 2n = 58-60, FN = 62-66 population identified as *O. yunganus*. This species is nearly identical with *O. capito*, especially externally, but may be distinguished by the comparatively narrow incisive foramina and the presence of an enamel island in the second upper molars separating the first primary and major folds (first internal fold discrete). These molars differ from those of *O. nitidus* (another species with enamel islands) in that the first internal fold is usually coalesced with medial portions of the first secondary fold. While also superficially similar to *O. nitidus* in the shape of the incisive foramina, *O. yunganus* differs from both *O. nitidus* and *O. capito* in smaller overall size and a marked tendency for lateral as well as medial development of palatal excrescences.

The holotype of *Oryzomys rivularis* (BM 1. 1. 6. 5.) has the long orbital vibrissae (about 45 mm in length) and the thick, close fur texture characteristic of *O. bombycinus* Goldman, 1911 and may prove to be the same species. If it does, *O. rivularis* J. A. Allen, 1901 has priority. *Oryzomys rivularis* was considered a synonym of *O. laiceps*, which later became *O. capito*, by Hershkovitz (1960:544). Pine (1971) reported *O. bombycinus* from Ecuadorian localities close to the type locality of *O. rivularis* (Rio Verde, Prov.
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Esmeraldas, Ecuador), but he did not mention O. rivularis in his review of the taxonomy of O. bombayinus.

The Oecomys concolor (chromosomal variant 2) from Villavicencio, Colombia are topotypes of Oryzomys belvulosus Allen (Oryzomys vicencianus Allen, with the same type locality, is a synonym, and both are treated as synonyms of Oryzomys (Oecomys) concolor concolor by Hershkovitz, 1960).

Among the other cricetine taxa collected and karyotyped at Villavicencio was a male Holochilus brasiliensis (2n=50, FN=58). Another specimen from Villavicencio was found in the American Museum (AMNH 75240). This species has not previously been recorded from Colombia in the literature.

Recently, one of us (ALG) had the opportunity to make a brief and regrettably cursory examination of the holotype of Oryzomys borreroi in the Universidad Nacional de Colombia, Bogotá. Hernández (1957) described the species as a member of the subgenus Microneoncomys and more nearly related to Oryzomys dimidiatus than to other members of the genus. However, Hershkovitz (1966b:737, footnote; 1970:792) expressed the opinion that, judging by the original description, O. borreroi was not most closely related to O. dimidiatus, but did seem to be an Oryzomys. We suggest that O. borreroi is not an oryzomyine rodent and, on the basis of body proportions, fur texture, and dental morphology, we believe that it is best considered an out-sized member of the genus Zygodontomys. The holotype is the only known specimen.

Thomas (1927:549) designated Amable María as the type locality of O. nitidus. In the original description, Thomas (1884:447) located Amable María as "... situated between the streams of Chanchamayo and Anamayo, at a little distance from the river Tutamayo [sic] ..." Stiglich (1922:71) identified Amable María as a hacienda in the Provincia de Tarma, Distrito de Chanchamayo, in the Tulumayo Valley. Hershkovitz (1944:99) gave this locality as "... between the Ríos Chanchamayo and Vitoc, a short distance above the Tulumayo." However, uncertainty arises when Hershkovitz, on the same page, says that the name Río Chanchamayo is applied to the Río Perené above its junction with the Tulumayo. He also equates the Ríos Aynamayo (Anamayo of Thomas, 1884) and Vitoc, as did Vaurie (1972:7).

Confusion regarding the location of Amable María stems from the fact
that the names Chanchamayo, Tulumayo, and Perené have been applied to the same river; the names Chanchamayo, Vitoc, and Anamayo have applied to streams emptying into the Tulumayo; and the name Chanchamayo has been applied to the small settlement located at the junction of the Vitoc with the Río Tulumayo (Hershkovitz, 1944:99), to the upper Río Perené below San Ramón (Vaurie, 1972), or to the region encompassing the Tulumayo and Perené River Valley, whose center is La Merced de Chanchamayo (Stiglich, 1922; Vaurie, 1972).

One of us (ALG) visited this region in November, 1974, and found that according to local informants Amable María is a small community in the Tulumayo Valley about 10 kilometers south of San Ramón and separated by a series of ridges from the Río Tulumayo, which lies to the east. Therefore, the approximate coordinates of 11° 10' S, 75° 19' W given by Vaurie (1972:6) are very close indeed. The village where the Vitoc empties into the Río Tulumayo, usually shown on maps as Pueblo Nuevo and referred to as Chanchamayo by Hershkovitz (1944:99), is locally known as Vitoc and is 13.4 kilometers by road south of San Ramón.

As certain of the other localities mentioned in this report appear on few maps or none at all, we shall give their locations.

Balta (10° 08'S, 71° 13'W), on Río Curanja, ca. 300 m, Depto. Loreto, Perú. A small Cashinahua Indian village on the Río Curanja, a tributary of the Río Alto Purus.

Cariari (10° 22'N, 83° 31'W), on Río Tortuguero, ca. 100 m, Prov. Limón, Costa Rica. An Instituto de Tierras y Colonización (ITCO) colony north of Guápiles.

Cordillera Carpish, Depto. Huánuco, Perú. The mountain range between Huánuco and Tingo María. A camp (09° 42'S, 76° 04'W), ca. 2,400 m, on the eastern slope of the cordillera, along the Carretera Central, was the collecting site for specimens with this locality designation.

Huanhuachayo (12° 44'S, 73° 47'W), ca. 1,660 m, Depto. Ayacucho, Perú. A clearing along the Andean mule trail connecting Hacienda Luisiana and nearby communities along the Río Apurimac and Río Santa Rosa with the mountain town of Tambo.

Lomas de Lachay (near 11° 20'S, 77° 25'W), ca. 300 m, Depto. Lima, Perú.
Peñas Blancas (03° 25’N, 76° 35’W), on Río Pichindé, ca. 1,800 m, Depto. Valle, Colombia. In the upper watershed of the Río Pichindé about 18 km WSW Cali.

Río Palca, ca. 15 km W San Ramón, Depto. Junín, Perú. On Tarma-San Ramón highway.

San José (12° 44’S, 73° 46’W), on Río Santa Rosa, ca. 1,000 m, Depto. Ayacucho, Perú. A small settlement a short distance below Huanhuachayo on the Río Santa Rosa (see Huanhuachayo).

San Lorenzo, Cerros San Lorenzo, 2,200 m, Depto. Magdalena, Colombia. A forestry research station (INDERENA) in the Sierra de Santa Marta above Míncu.

Yuracryacu (12° 45’S, 73° 48’W), ca. 2,600 m, Depto. Ayacucho, Perú. A clearing along the Andean mule trail a short distance above Huanhuachayo (see Huanhuachayo).

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