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Alfred L. Gardner

James L. Patton

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

By ALFRED L. GARDNER[1] and JAMES L. PATTON[2]

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 Pascual, 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 habitus 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

[1] National Fish and Wildlife Laboratory, Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560.

[2] Museum of Vertebrate Zoology, University of California, Berkeley, Cailfornia 94720.

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 arduous 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, phyllotine, and oryzomyine rodents; in the latter are the thomasomyine, oxymycterine, scapteromyine, wiedomyine, and ichthyomyine groups. Only two recent comprehensive revisionary efforts (Pearson, 1958; Hershkovitz, 1962) have been attempted, and both have dealt principally with the phyllotines. Thus, detailed knowledge of species units and their geographic variation 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, 1955, 1960, 1962, and 1966a), and Hooper and Musser (1964).

In this paper, we are attempting a clarification of some of the species relationships within the oryzomyines in addition to summarizing their evolutionary trends as indicated by available karyotypic data. Our emphasis has been on clarifying the kinds and patterns of variation at this level and applying these interpretations to comparable data for the Sigmodontini 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, *Nectomys* Peters; and the spiny mice, *Neacomys* Thomas. *Oryzomys* includes at least eight subgenera for which chromosomal data from all but two (*Macruroryzomys* and *Micronectomys*) are now available. As demonstrated beyond, these data are indicative of the diversity of forms within the oryzomine complex 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*, *Nectomys*, 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 albigularis (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: $2n=66$, 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) $2n=66$, 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,

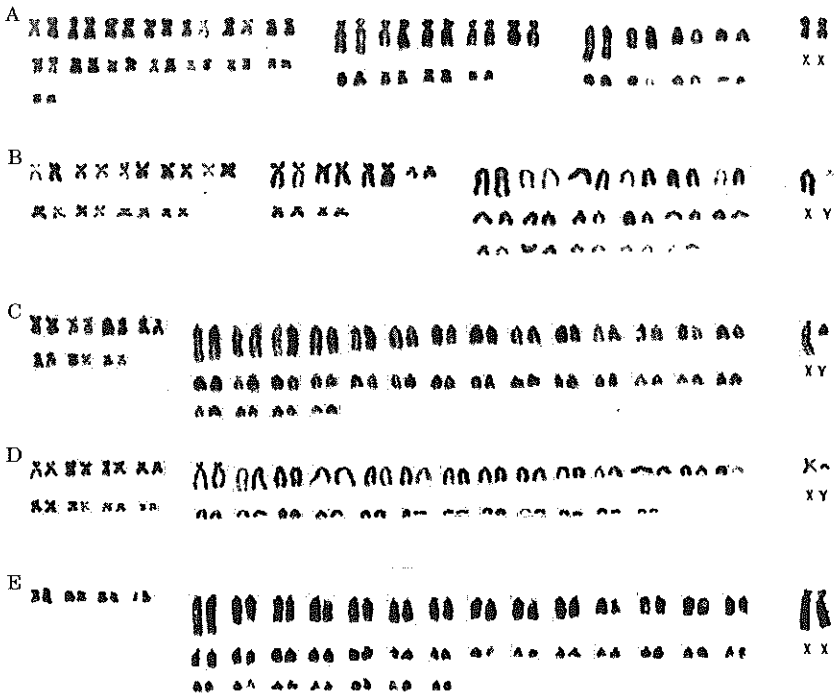

FIGURE 1. Representative karyotypes of members of the "*albigularis* chromosome group" of *Oryzomys* (s.s.). A) *Oryzomys albigularis* (Tomes), variant 1; $2n=66$, FN=112; female; San Lorenzo, Cerro San Lorenzo, Depto. Magdalena, Colombia; USNM 507238. B) *Oryzomys albigularis* (Tomes), variant 2; $2n=66$, FN=94; male; Peñas Blancas, Río Pichindé, Depto. Valle, Colombia; USNM 507242. C) *Oryzomys albigularis* (Tomes), variant 3; $2n=80$, FN=92; male; Yuraccyacu, Depto. Ayacucho, Perú; LSUMZ 16673. D) *Oryzomys auriventer* Thomas; $2n=70$, FN=84; male; Huanhuachayo, Depto. Ayacucho, Perú; LSUMZ 16667. E) *Oryzomys niditus* (Thomas); $2n=80$, FN=86; female; Balta, 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.

Specimens examined. COLOMBIA. Depto. Magdalena: San Lorenzo, Cerro San Lorenzo (3 males, 3 females—USNM 507225-27, and 507238-40).

(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) $2n=80$, 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.

Specimens examined. PERÚ. Depto. Junín: Río Palca, *ca.* 15 km. W San Ramón (1 female—USNM 507244). Depto. Ayacucho: Yuraccyacu (3 males, 3 females—LSUMZ 16670-75).

Oryzomys auriventer Thomas.—$2n=70$, 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, 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 Apurimac (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 yunganus Thomas (Fig. 2).—We have recorded two karyotypic variants of this species.

(1) $2n=60$, 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.

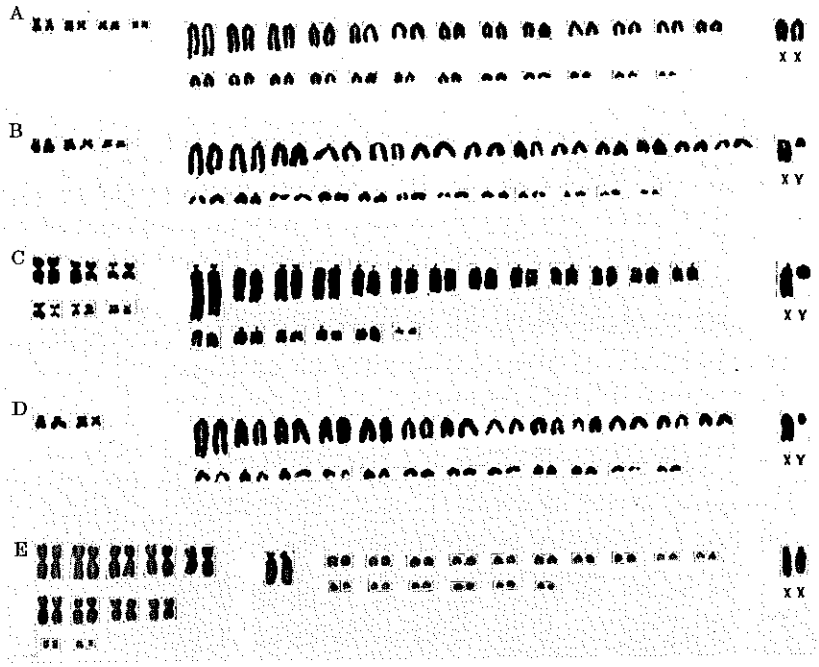

FIGURE 2. Representative karyotypes of members of the "*palustris* chromosome group" (A-D) and "*bombycinus* chromosome group" of *Oryzomys* (s.s.). A) *Oryzomys yunganus* Thomas, variant 1; $2n=60$, FN=66; female; San José, Río Santa Rosa, Depto. Ayacucho, Perú; LSUMZ 16689. B) *Oryzomys yunganus* Thomas, 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 xanthaeolus* Thomas; $2n=56$, FN=58; male; 2 mi. W Porculla Pass, Depto. Lambayeque, Perú; MVZ 137943. E) *Oryzomys bombycinus* 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.

Specimens examined. PERÚ: Depto. Loreto: Balta, Río Curanja (2 males—MVZ 136585 and 136587).

Oryzomys capito (Olfers).—$2n=52$, 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. PERÚ. 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 14358, 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 25 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.

Specimens examined. MÉXICO. Nayarit: 8 mi. E San Blas (1 male—LSUMZ 11980). Chiapas: 3 km. E Risa de Oro (1 male, 2 females—LSUMZ 11981-83).

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. PERÚ. 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 Chilca (1 male, 1 female—MVZ 137592-93).

Oryzomys bauri 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 bombycinus 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, Río 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; Huanhuachayo, 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 referrable 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 Puquio (1 female —MVZ 139219).

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

Specimens examined. PERÚ. Depto. Ayacucho: Hda. Luisiana, Río Apurimac (2 males, 1 female—LSUMZ 16695-96 and 16699). Depto. Loreto: Balta, Río Curanja (9 males, 8 females—LSUMZ 14360; MVZ 136581, 136594, 136596-98, 136600, 136602-04, 136606-08, 136610-12, and 136615).

(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. Bolivar: (1 female—courtesy of O. A. Reig and P. Kiblisky).

(4) $2n=60$; FN=76 (Fig. 3D). *Autosomes*: 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); Huanhuachayo (2 males—LSUMZ 16697 and 16701).

Oryzomys andinus Osgood.—$2n=60$; FN=70 (Fig. 3E). *Autosomes*: 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.

Specimen examined. PERÚ. Depto. Ancash: 2 mi. W Yupash (1 male—MVZ 139218).

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

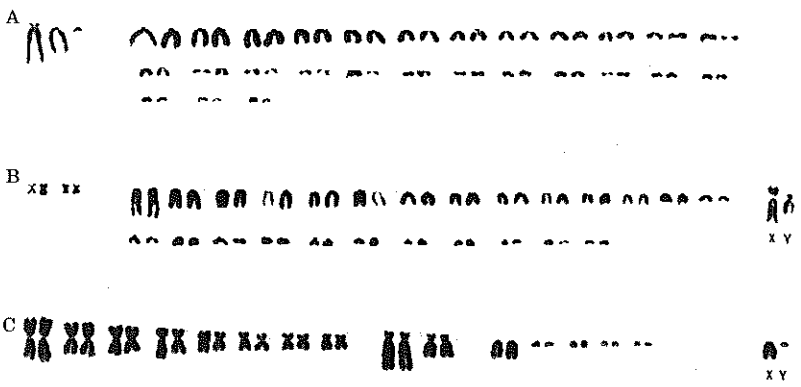

FIGURE 4. Representative karyotypes of members of the subgenera *Microryzomys* (A) and *Melanomys* (B), and the genus *Nesoryzomys* (C). A) *Oryzomys minutus altissimus* Osgood; $2n=57$, FN=(58); female; 4 mi. S, 8 mi. E Recuay, Depto. Ancash, Perú; MVZ 137924. B) *Oryzomys caliginosus* (Tomes); $2n=56$, FN=58; male; Cariari, Prov. Limón, Costa Rica; LSUMZ 13192. C) *Nesoryzomys narboroughi* 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 *Microryzomys* 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=32) possessed an uneven diploid number of 57. A diploid number of 58 has been reported for a male of this species from Venezuela (Kiblisky, 1969:1339).

Specimen examined. PERÚ. Depto. Ancash: 4 mi. S, 8 mi. E Recuay (1 female—MVZ 137924).

Subgenus *Melanomys* Thomas

Oryzomys caliginosus (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.

Specimens examined. COSTA RICA. Prov. Limón: Cariari (4 males, 2 females—LSUMZ 13186, 13190-92, and 13194-95). Prov. Cartago: Pacuare, Río Pacuare (1 male—LSUMZ 13188).

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.

Specimens examined. COSTA RICA. Prov. Limón: Cariari (1 male, 1 female—LSUMZ 13199-200). Prov. Cartago: Pacuare, Río Pacuare (1 male —LSUMZ 13201).

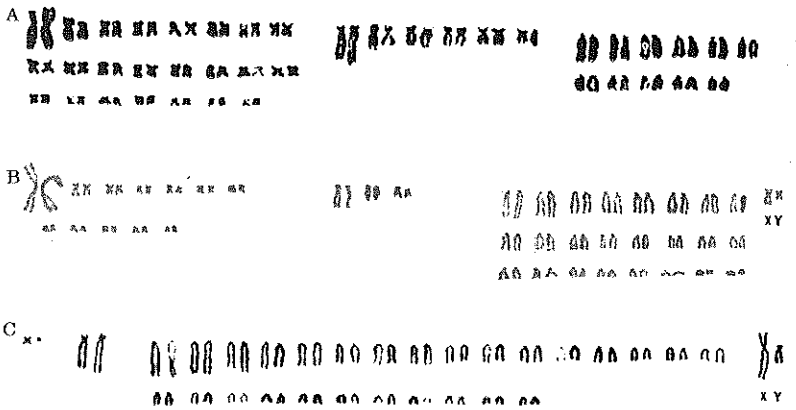

FIGURE 5. Representative karyotypes of members of the genus *Oecomys*. A) *Oecomys bicolor* (Tomes); $2n=80$, FN=134 or 136; female; Balta, Río Curanja, Depto. Loreto, Perú; MVZ 136592. B) *Oecomys concolor* (Wagner), variant 1; $2n=80$, FN=112; male; Balta, Río Curanja, Depto. Loreto, Perú; LSUMZ 16676. 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.

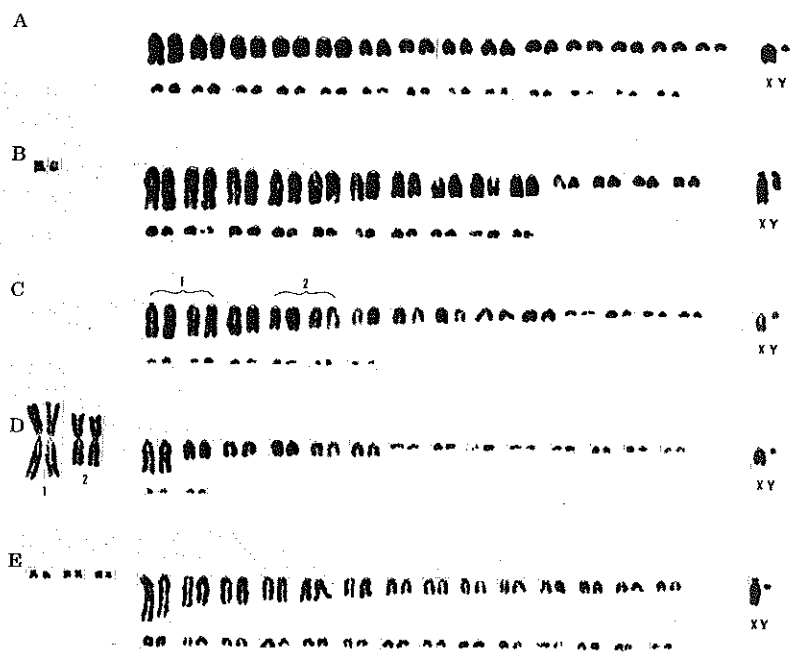

FIGURE 6. Representative karyotypes of members of the genera *Oryzomys* (*Sigmodontomys*), *Nectomys*, and *Neacomys*. A) *Oryzomys alfari* (J. A. Allen); $2n=56$, FN=54; male; Pacuare, Río Pacuare, Prov. Cartago, Costa Rica; LSUMZ 13201. B) *Nectomys squamipes* (Brants), variant 1; $2n=52$, FN=52; male; Yarinacocha, Depto. Loreto, Perú; LSUMZ 14374. C) *Nectomys squamipes* (Brants), variant 2; $2n=42$, FN=40; male; Balta, Río Curanja, Depto. Loreto, Perú; MVZ 136641. D) *Nectomys squamipes* (Brants), variant 3; $2n=38$, FN=40; male; Hda. Luisiana, Río Apurimac, Depto. Ayacucho, Perú; LSUMZ 16711. E) *Neacomys spinosus* (Thomas); $2n=64$, FN=68; male; Balta, Río Curanja, Depto. Loreto, Perú; MVZ 139185.

Specimen examined. PERÚ. Depto. Loreto: Balta, Río Curanja (1 male—LSUMZ 16676).

(2) $2n=60$; FN=62 (Fig. 5C). *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.

Specimens examined. COLOMBIA. Intend. Meta: Finca Buque, Villavicencio (6 males, 2 females—USNM 507247-54).

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 Apurimac (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 chromosomes*: X, a large subtelocentric; Y, a small acrocentric.

Specimens examined. COLOMBIA. Intend. Meta: Finca Buque, Villavicencio (1 male, 1 female—USNM 507259-60). PERÚ. Depto. Ayacucho: San José, Río Santa Rosa (1 male, 1 female—LSUMZ 16702-03). Depto. Loreto: Balta, Río Curanja (7 males, 5 females—MVZ 136617-19, 136621-26, 136633, 136636, and 139185).

KARYOTYPIC AFFINITIES

The oryzomyine group of Neotropical cricetines is karyotypically multiform. 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,

1968, 1972; Simpson, 1950, 1969) seems unlikely and is not supported by karyotypic data.

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 karotypic data in identifying taxonomic units and in elucidating cricetine relationships.

Perhaps the most comprehensive group includes *O. palustris*, *O. yunganus* (chromosomal variants 1 and 2), *O. capito*, *O. xanthaeolus*, *O. bauri*, and *O. macconnelli* of the nominate subgenus, along with *O.* (*Melanomys*) *caliginosus*, and *O.* (*Microryzomys*) *minutus*. 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. albigularis*) 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 traplines with *O. macconnelli* at Balta, Depto. Loreto, Perú. *Oryzomys bauri* and *O. xanthaeolus* are obviously closely related. Indeed, the mainland *O. xanthaeolus* is the most logical ancestor of the Galapagoan *O. bauri* and *O. galapagoensis* on chromosomal as well as on morphological grounds.

Nectomys (*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 *Nectomys* (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 glandes 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*) *alfari* 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. albigularis* (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. albigularis*. 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. albigularis* (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. albigularis* differs from that of the Rancho Grande form in having four more pairs of biarmed autosomes, four fewer pairs of uniarmed 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. albigularis* are forest inhabitants occurring at middle to upper elevations. The only karyotypic similarities held in common with the Venezuelan *O.*

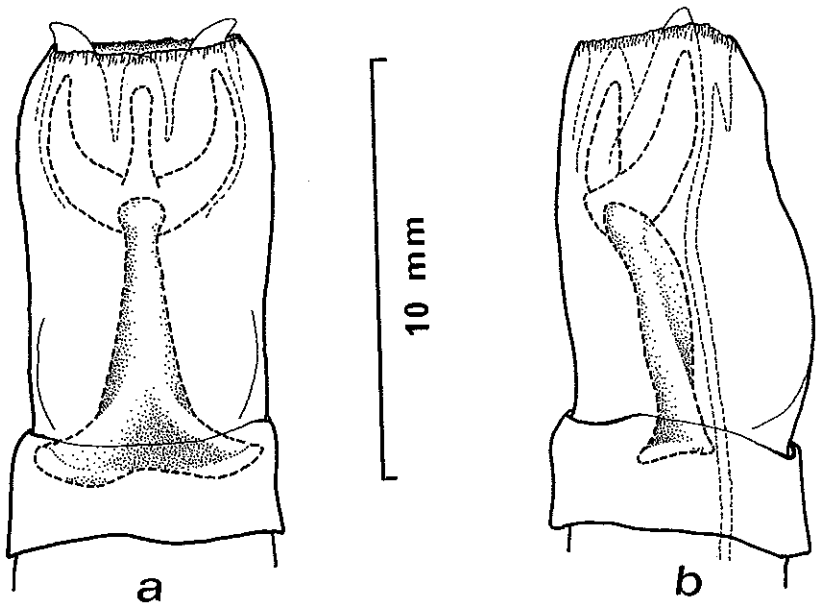

FIGURE 7. The glans penis of *Nectomys squamipes*, Balta, Río Curanja, Depto. Loreto, Perú; MVZ 136641: *a*, ventral view; *b*, lateral view.

albigularis are in the diploid number (66) and the morphology of the X chromosome. The San Lorenzo *Oryzomys*, originally described as *O. maculiventer* J. A. Allen, constitute a distinctive morphological and karyotypic race of the 66-chromosome form of *O. albigularis*.

Oryzomys auriventer (Fig. 1D) is clearly affiliated with the *O. albigularis* group and karyotypically is closest to the Venezuelan *O. albigularis* reported on by Kiblisky (1969). We do not doubt, however, that *O. auriventer* is a full species, as it occurs sympatrically with *O. albigularis* in parts of its range.

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. yunganus*, *O. macconnelli*, and particularly *O. capito* (a species with which it is commonly confused). Hershkovitz (1966a:138) considered *O. nitidus* as representing *O. alfaroi* (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 *Nesoryzomys*, 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 biarms 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. narboroughi* (Fig. 4C) has the lowest diploid number (32) and, next to the chromosomal variants 2 and 3 of *Nectomys 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), sigmondonts (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 multiform 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*, *Eligmodontia*, *Neotomys*, and *Reithrodon*; and the closely related polytypic *Phyllotis*, *Graomys*, and *Aulis-*

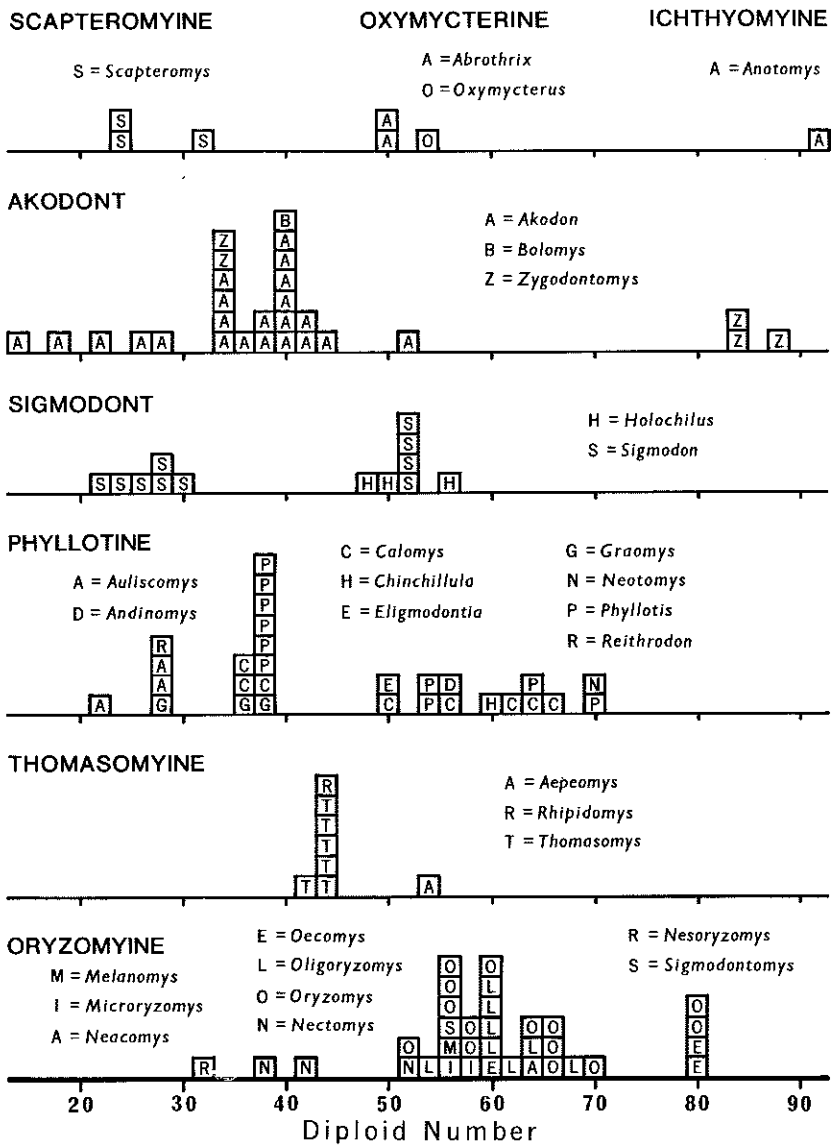

FIGURE 8. Summary of distribution of diploid numbers for taxa representing eight of the nine recognized suprageneric groups of Neotropical cricetines. Data taken from Tables 1 and 2.

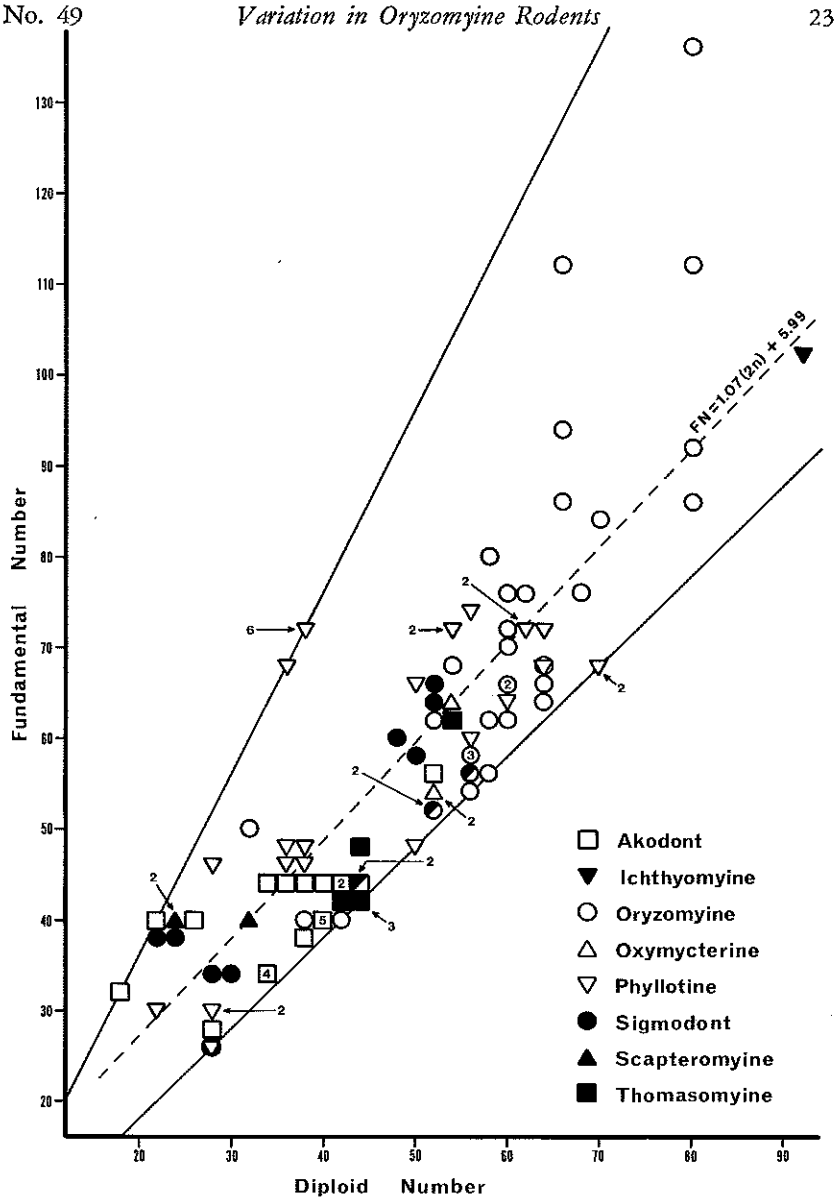

FIGURE 9. Bivariate plot of fundamental number and diploid number for each of the chromosomally known taxa of Neotropical cricetines. Solid lines delimit maximum and minimum values for fundamental numbers possible at any given diploid number.

TABLE 1.—KARYOTYPIC DATA FOR ORYZOMYINE RODENTS

Taxon	N ♂	N ♀	2n	FN	autosome pairs biarms	autosome pairs uniarms	X	Y	Karyotypes not described herein
Oryzomys (*Oryzomys*)									
albigularis	2	3	66	86	11	21	M	SM	Kiblisky, 1969
albigularis (1)	3	3	66	112	24	8	M	SM	
albigularis (2)	2	1	66	94	15	17	A	SM	
albigularis (3)	3	4	80	92	7	32	ST	A	
auriventer	1	2	70	84	8	26	M	SM	
nitidus	8	5	80	86	4	35	ST	A	
yunganus (1)	1	2	60	66	4	25	A	A	
yunganus (2)	2	—	58	62	3	25	A	A	
capito	15	7	52	62	6	19	A	A	
palustris	2	2	56	56	1	26	A	A	Hsu et al., 1969
xanthaeolus	3	3	56	58	2	25	A	A	
bauri	3	3	56	58	2	25	A	A	
macconnelli	—	1	64	64	1	30	A	A	
bombycinus	2	3	58	80	12	16	ST	A	
Oryzomys (*Oligoryzomys*)									
longicaudatus (1)	—	1	68	(78)	5	29	?	?	
longicaudatus (2)	11	9	64	66	2	29	ST	A	
longicaudatus (3)	—	1	62	(78)	8	23	?	?	
longicaudatus (4)	3	1	60	76	9	20	SM	M	
andinus	1	—	60	70	6	23	A	A	
delicatus	3	—	60	72	7	22	ST	ST	Kiblisky, 1969
flavescens	?	?	60	66	4	25	SM	A	Brum, 1965
fulvescens	1	—	54	68	8	18	A	A	
Oryzomys (*Microryzomys*)									
minutus altissimus	—	1	57	(58)	(1)	27	?	?	
minutus	1	—	58	?	?	?	?	?	Kiblisky, 1969
Oryzomys (*Melanomys*)									
caliginosus	5	2	56	58	2	25	ST	ST	
Oryzomys (*Sigmodontomys*)									
alfari	2	1	56	54	—	27	A	A	
Nesoryzomys									
narborough	3	3	32	50	10	5	A	A	
Oecomys									
bicolor	—	4	80	(138)	29	11	?	?	
concolor (1)	1	—	80	112	12	27	SM	M	
concolor (2)	6	2	60	62	2	27	SM	ST	
Nectomys (*Nectomys*)									
squamipes (1)	2	2	52	52	1	24	ST	ST	
squamipes (2)	1	—	42	40	—	20	A	A	
squamipes (3)	2	2	38	40	2	16	A	A	
Neacomys spinosus	9	7	64	68	3	28	ST	A	

comys. The inclusion of *Neotomys* and *Reithrodon* (members of the sigmodont group, sensu Hershkovitz, 1962) within the phyllotines was principally based on shared karyotypic features. In addition—particularly for *Reithrodon*—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 lasiurus*, 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 leander*. 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 *Nectomys squamipes* (variants 2 and 3) of the oryzomyine complex, *Graomys* and *Calomys* of the phyllotines, and most of the thomasomyines.

Bianchi et al. (1971:724) cite Oswaldo Reig as recommending full generic recognition for *Abrothrix*, *Akodon*, *Blarinomys*, *Bolomys*, *Chroeomys*, *Hypsimys*, *Lenoxus*, *Microxus*, *Notiomys*, *Oxymycterus*, *Podoxymys*, *Talpomys*,

TABLE 2.—SUMMARY OF KARYOTYPIC DATA FOR NON-ORYZOMYINE NEOTROPICAL CRICETINES.

Taxon	2n	FN	X	Y[1]	Reference[2]
thomasomyine group					
Rhipidomys latimanus	44	48	A	A	Colombia: Peñas Blancas (USNM)
Thomasomys monochromos	42	42	SM	A	Colombia: San Lorenzo (USNM)
Thomasomys aureus	44	42	A	A	Perú: Río Palca (USNM); Yuraccyacu (LSUMZ)
Thomasomys sp.	44	42	SM	SM	Ecuador: Mt. Pichincha (MVZ)
Thomasomys kalinowskii	44	44	A	A	Perú: Yuraccyacu (LSUMZ)
Thomasomys notatus	44	44	A	A	Perú: Cordillera Carpish (LSUMZ)
Thomasomys taczanowski	44	44	A	A	Perú: Yuraccyacu (LSUMZ)
Aepeomys fuscatus	54	62	SM	SM	Colombia: Peñas Blancas (USNM)
scapteromyine group					
Scapteromys aquaticus	32	40	ST	A	Gentile de Fronza, 1970a
Scapteromys tomentosus	24	40	SM	A	Brum, 1965
Scapteromys tumidus	24	40	A	A	Brum et al., 1973
phyllotine group					
Phyllotis osilae	70	68	A	A	Pearson, 1972
Phyllotis andium	64	72	SM	SM	"
Phyllotis definitus	54	72	SM	A	"
Phyllotis wolffsohni	54	72	M	SM	Pearson and Patton, in press
Phyllotis magister	38	72	SM	A	Pearson, 1972
Phyllotis gerbillus	38	72	SM	A	"
Phyllotis darwini	38	72	SM	SM	"
Phyllotis amicus	38	72	A	SM	"
Phyllotis caprinus	38	72	SM	M	Pearson and Patton, in press
Phyllotis haggardi	38	72	SM	SM	Pearson, 1972
Auliscomys pictus	28	30	A	A	"
Auliscomys sublimis	28	30	A	A	"
Auliscomys boliviensis	22	30	A	A	Pearson and Patton, in press

Graomys domorum	28	46	A	A	"
Graomys griseoflavus	36-38	46	SM	A	Pearson and Patton, in press; Wainberg and Gentile de Fronza, 1974
Calomys sorellus	64	68	ST	A-ST	Pearson and Patton, in press
Calomys laucha	56	60	SM	A	Brum, 1965
Calomys laucha	62	72	A	A	Massoia et al., 1968
Calomys fecundus	50	66	SM	A	Pearson and Patton, in press
Calomys musculinus	38	48	A	A	Massoia et al., 1968
Calomys lepidus	36	68	SM	ST	Pearson and Patton, in press
Calomys callosus	66	?	?	?	Matthey, 1968
Calomys callosus	36	48	M	A	Pearson and Patton, in press
Eligmodontia typhus	50	48	A	SM	"
Andinomys edax	56	(76)	?	?	"
Chinchillula sahamae	60	64	SM	M-SM	"
Neotomys ebriosus	70	68	ST	SM	"
Reithrodon physodes	28	26	SM	A	Brum, 1965
ichthyomyine group					
Anotomys leander	92	(102)	?	?	Gardner, 1971
akodont group					
Akodon jelskii	52	(58)	?	?	Perú: Depto. Puno (MVZ); Depto. Lima (MVZ)
Akodon molinae	42-43	44	A	A	Bianchi et al., 1971
Akodon illuteus	41	(44)	?	?	"
Akodon boliviensis	40	40	A	A	"
Akodon boliviensis	40	(46)	?	?	Perú: Depto. Puno (MVZ); Depto. Tacna (MVZ); Depto. Apurimac (MVZ)
Akodon berlepschii	40	40	A	A	Perú: Depto. Tacna (MVZ)
Akodon varius	40	40	ST	SM	Bianchi et al., 1971; Paraguay: Depto. Boquerón (MVZ)
Akodon aerosus	40	40	SM	ST	Perú: Hda. Luisiana (LSUMZ); San José (LSUMZ); Huanhuachayo (LSUMZ); Vitoc (USNM); Río Palca (USNM)

TABLE 2. Continued

Taxon	2n	FN	X	Y[1]	Reference[2]
Akodon dolores	38	44	A	A	Bianchi et al., 1971
Akodon azarae	38	38	A	A	Bianchi and Contreras, 1967; Bianchi et al., 1968, 1971
Akodon sp.	34-35	44	A	A	Bianchi et al., 1971
Akodon amoenus	34	34	A	SM	Perú: Depto. Puno (MVZ)
Akodon arviculoides	34	34	A	A	Bianchi et al., 1971; Yonenaga and Ricci, 1969
Akodon arviculoides	14	?	?	?	Yonenaga, 1973
Akodon obscurus	34	34	A	A	Bianchi et al., 1971
Akodon obscurus	28	29	SM	A	Brum, 1965
Akodon orophilus	26	40	SM	ST	Hsu and Benirschke, 1973
Akodon sp.	22	40	SM	SM	Ecuador: Prov. Pichincha (MVZ); Perú: Depto. Ancash (MVZ)
Akodon urichi	18	32	SM	A	Reig and Kiblisky, 1968; Reig et al., 1971
Bolomys albiventer	40	40	A	A	Bianchi et al., 1971
Zygodontomys microtinus	88	?	?	?	Colombia: Villavicencio (USNM)
Zygodontomys microtinus	84	?	?	?	Kiblisky et al., 1970
Zygodontomys brevicauda	84	?	?	?	Costa Rica: Parrita (LSUMZ)
Zygodontomys lasiurus	34	?	?	?	Yonenaga, 1973
Zygodontomys sp.	34	34	A	A	Paraguay: Depto. Boquerón (MVZ)
oxymycterine group					
Oxymycteris rutilans	54	64	SM	A	Gentile de Fronza, 1970b
Abrothrix longipilis	52	54	ST	A	Bianchi et al., 1971
Abrothrix xanthorhinus	52	54	ST	A	"
sigmodon group					
Sigmodon hispidus	52	52	ST	SM	Hsu and Benirschke, 1968; Kiblisky, 1969; Zimmerman, 1970; Zimmerman and Lee, 1968
Sigmodon leucotis	52	52	A	A	Zimmerman, 1970
Sigmodon alleni	52	64	ST	SM	"
Sigmodon ochrogaster	52	66	ST	ST	"

Sigmodon fulviventer	28-30	34	A	A	Hsu and Benirschke, 1969; Lee and Zimmerman, 1969
Sigmodon mascotensis	28	26	A	A	Zimmerman, 1970
Sigmodon arizonae	22-24	38	A	A	Hsu and Benirschke, 1973; Zimmerman, 1970; Zimmerman and Lee, 1968
Holochilus brasiliensis	56	56	A	A	Perú: Hda. Luisiana (LSUMZ)
Holochilus brasiliensis	50	58	A	M	Colombia: Villavicencio (USNM)
Holochilus brasiliensis	48	60	SM	A	Paraguay: Depto. Cordillera (MVZ)

[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 albiventer*) 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. xanthorhinus* 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 *Oryzomys 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 phyllotines (*Graomys*). We remark on this association without implying any particularly close phyletic affinity. But, since *Scapteromys* is karyotypically unlike any oryzomyine, thomasomyine, 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 *Reithrodon* is closest to the phyllotines, *Holochilus* is closest to the oryzomyines, and both are distinct from *Sigmodon* (and *Sigmomys*). Pearson and Patton reached the same conclusion regarding *Reithrodon*, and placed it near *Auliscomys*. They also included *Neotomys* within the phyllotines, stressing its chromosomal similarities with *Phyllotis 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 *Reithrodon 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, *Reithrodon physodes* is also similar to *Sigmodon mascotensis* as well as *Auliscomys*, differing from the former primarily in the morphology of the X chromosome. Therefore, *Reithrodon* 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 *Reithrodon* and some species of *Sigmodon* 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 oryzomyines suggested by Hooper and Musser (1964). Indeed, the Peruvian specimens are nearly identical chromosomally to several species of both *Oryzomys* and *Sigmodon*. The differences in cranial and dental structures, however, would seem to refute any close relationship with the oryzomyine group.

The chromosomal and morphological evidence at hand supports the hypothesis that *Neotomys* and *Reithrodon* are phyllotines. The suite of characters linking *Neotomys* and *Reithrodon* to the phyllotines would appear to override the significance of their similarities with *Sigmodon* 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 thomasomyine group (sensu Hershkovitz, 1966a:125) includes *Thomasomys*, *Rhipidomys*, *Nyctomys*, *Otonyctomys*, and *Phaenomys*. Members of this group represented by our material (Table 2) include *Rhipidomys latimanus* and at least six species of *Thomasomys* (sensu lato). *Aepeomys* (=*Thomasomys*) *fuscatus* ($2n=54$, FN=62) is karyotypically the most aberrant representative and actually may not belong in the *Rhipidomys* and *Thomasomys* complex. Therefore, we are using the generic name *Aepeomys* 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 thomasomyine species comprise a uniform assemblage characterized by a diploid number of 42 or 44 and a predominantly all acrocentric autosomal complement. *Thomasomys monochromos* 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 thomasomyines 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 *Aepeomys fuscatus*, the thomasomyines 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 heterochro-

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., *Phyllotis, Auliscomys*, 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 *Anotomys 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

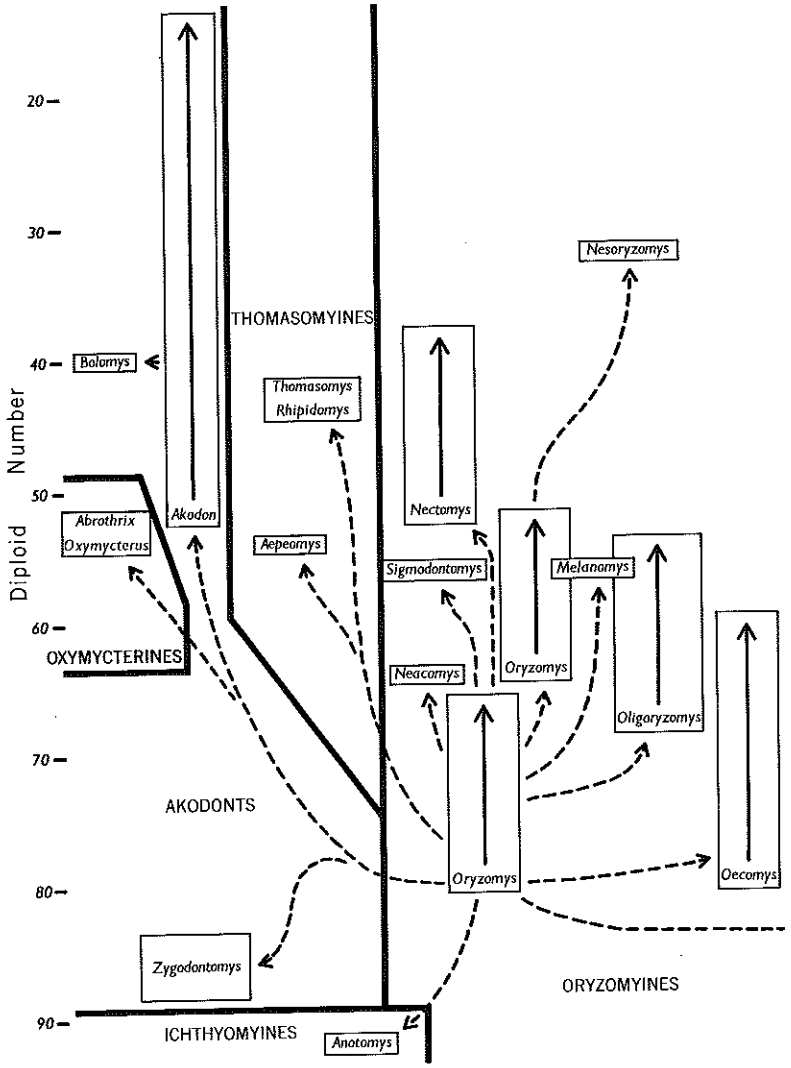

FIGURE 10. (part).

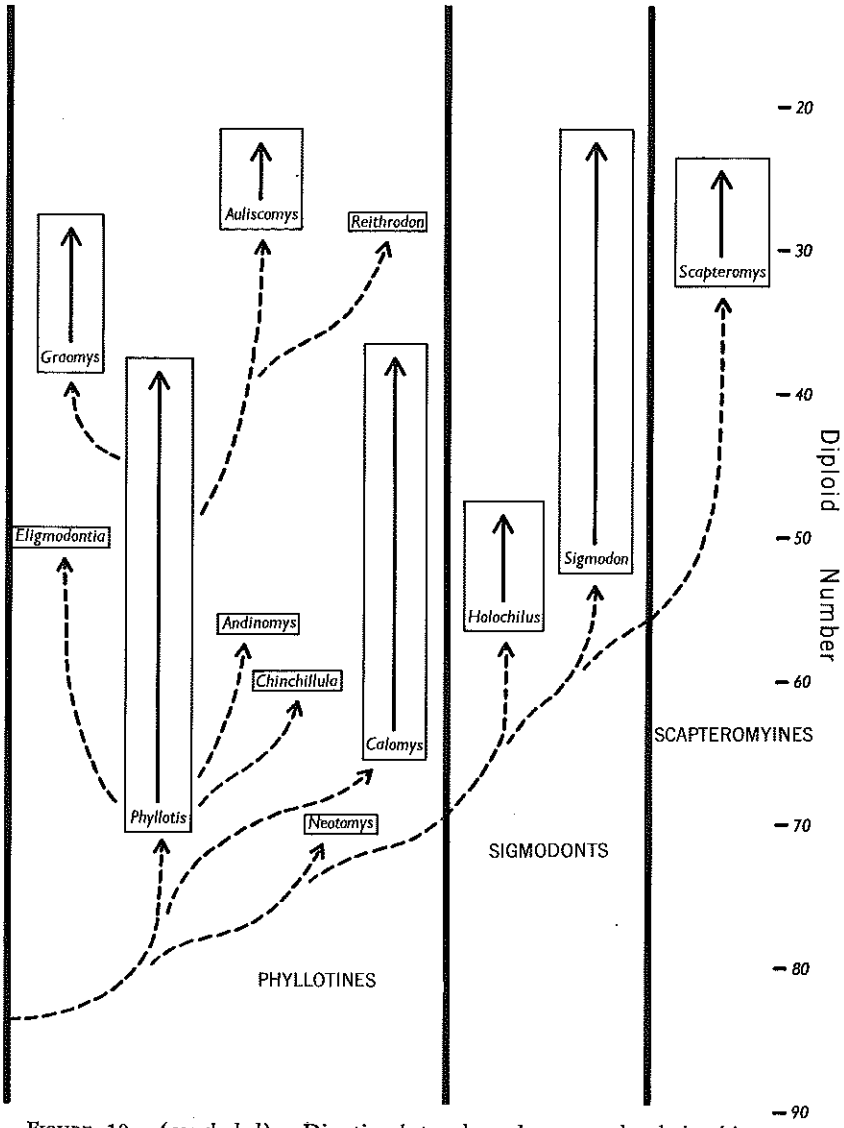

FIGURE 10. (concluded). Directional trends and suggested relationships among the Neotropical cricetines based primarily on karyotypic data, but also including an appreciation for cranial, dental, and phallic morphologic characters and zoogeographic considerations.

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 phyllotines). Furthermore, specialists on the akodonts or phyllotines 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 concommitant 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 *Phyllotis* 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 congeners 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 arizonae*, *Auliscomys boliviensis*, *Scapteromys tomentosus*, *Scapteromys tumidus*, and *Reithrodon physodes* represent the most specialized yet known among the Neotropical cricetine 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 domorum*, *Calomys lepidus*, *Sigmodon arizonae*, *Akodon urichi*, and the six $2n=38$, FN=72 species of *Phyllotis* have achieved the derived and highly specialized karyotypic state of totally biarmed autosomal complements (high FN/$2n$ ratios). This condition is approached by *Nesoryzomys narboroughi*, *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 cricetines.—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., *Oecomys*) and others are slightly to moderately modified for aquatic existence (e.g., *Nectomys*). 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 *Oryzomys* (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 phyllotines or sigmodonts than are shown in Figure 10. The phyllotine genera are arranged as in Pearson and Patton (in press), but note that *Neotomys* is shown as annectent 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 albigularis* (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. albigularis*. With the exception of *O. albigularis 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. albigularis* (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 *maculiventer*). 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. auriventer* as a full species distinct from *O. albigularis*. Our Huanhuachayo specimens are nearly identical with the holotype. *Oryzomys auriventer nimbosus* is also similar, but markedly smaller. *Oryzomys auriventer* is closest chromosomally to the $2n=66$ *O. albigularis* 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. albigularis* (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. albigularis* must await karyotypic information from topotypical material. The type locality of *O. albigularis* (Pallatanga, 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. keaysi*. Therefore, we suspect that the name *albigularis* 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. perenensis*. Other probable specific synonyms are *carrikeri*, *castaneus*, *magdalenae*, *medius*, *modestus*, *mollipilosus*, *oniscus*, *talamancae*, and *velutinus*.

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 *bolivaris* 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 cotype (BM 89. 5. 20. 1) is also like *O. nitidus*; therefore, *bolivaris* 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. albigularis*-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. laticeps*, 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* (Río Verde, Prov.

Esmeraldas, Ecuador), but he did not mention *O. rivularis* in his review of the taxonomy of *O. bombycinus*.

The *Oecomys concolor* (chromosomal variant 2) from Villavicencio, Colombia are topotypes of *Oryzomys helvolus* 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 *Micronectomys* 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 outsized 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 Rios 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 Rios 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 Guapiles.

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 Minca.

Yuraccyacu (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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