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KARYOLOGY OF *AEPEOMYS* AND *THOMASOMYS* (RODENTIA: MURIDAE) FROM THE VENEZUELAN ANDES

MARISOL AGUILERA M.,* ANTONIO PÉREZ-ZAPATA, JOSÉ OCHOA G., AND PASCUAL SORIANO

Universidad Simón Bolívar, Departamento de Estudios Ambientales, Apartado 89000, Caracas 1080-A, Venezuela (MAM, AP-Z)
Asociación Venezolana para la Conservación de Areas Naturales, Apartado 69520, Caracas 1063-A, Venezuela (JOG)
Universidad de Los Andes, Facultad de Ciencias, La Hechicera, Mérida 5101, Venezuela (PS)

We provide new data on the karyologic patterns of the Andean rodents *Aepeomys* and *Thomasomys,* including the 1st karyotypic description of *A. lugens* and *T. vestitus.* Two differentiated chromosomal formulae were found for *Aepeomys* in Venezuela; they are a diploid chromosome number (2n) = 28, fundamental number (FN) = 48 karyotype corresponding to *A. lugens* and a 2n = 44; FN = 46 karyotype for an unnamed population (*Aepeomys* sp.). According to the structure of these 2 karyotypes and the distribution of constitutive heterochromatin (scarce and restricted to a few chromosomes in *A. lugens* versus abundant and scattered among chromosomes in *Aepeomys* sp.), we suggest that *Aepeomys* sp. is a more primitive form than *A. lugens. T. laniger* and *T. vestitus* showed karyotypes of 2n = 42, FN = 40 and 2n = 44, FN = 42, respectively; the latter has an additional pair of small-sized metacentric chromosomes and an acrocentric X chromosome (metacentric in *T. laniger*). Our results suggest that *Aepeomys* and *Thomasomys* are closely related taxa in terms of their karyologic patterns.

Key words: *Aepeomys,* Andes, evolution, karyotype, rodents, *Thomasomys*

Despite various taxonomic reviews of tribes and genera of South American sigmodontine rodents (family Muridae), systematics of this group remain unclear, and several authors agree on the need for a thorough revision of most taxa (Musser and Carleton 1993; Reig 1981, 1986; Voss 1988, 1991; Voss and Emmons 1996). According to Reig (1986), *Thomasomys* and *Aepeomys* are members of the Oryzomyini tribe, 1 of the 3 numerically dominant tribes differentiated directly from the 1st sigmodontines that invaded South America, which have the most primitive dental and skull characteristics. However, Voss (1993) postulated that ''thomasomyines'' are primarily diagnosable by primitive character states, and therefore may be basal sigmodontines, not a real (monophyletic) group. Oryzomyines, on the other hand, can be diagnosed phylogenetically and seem likely to be monophyletic (Voss and Carleton 1993).

The Oryzomyini tribe is composed of 13 genera (Reig 1981); some are species-rich (e.g., *Oryzomys,* 36 species; *Thomasomys,* 27 species), others are moderately so (e.g., *Oecomys,* 13 species; *Rhipidomys,* 14 species), and the rest include 1–5 species. *Aepeomys* belongs to the latter, including only 2 described species (Musser and Carleton 1993). An essentially similar number of species per genus in the Oryzomyini has been reported by Musser and Carleton (1993).

* *Correspondent: maguiler@usb.ve*

Thomasomys and *Aepeomys* are good representatives of the general taxonomic ambiguity in several sigmodontine taxa, because some authors put them into different genera (Gyldentolpe 1932; Honacki et al. 1982; Musser and Carleton 1993; Reig 1986; Tate 1932) and others consider *Aepeomys* as a synonym of *Thomasomys* (Cabrera 1961; Ellerman 1941; Handley 1976). Gardner and Patton (1976) followed Hershkovitz (1966) in postulating that *Thomasomys* and *Aepeomys* together with *Rhipidomys, Nyctomys, Otonyctomys,* and *Phaenomys* compose the thomasomyine group. Analysis of the karyologic data of Gardner and Patton (1976) on 6 species of *Thomasomys* and 1 species of *Aepeomys* (*A. fuscatus* from Colombia), showed that those genera had very different karyotypes (diploid chromosome number [2n] = 42–44 and 2n = 54, respectively), and they argued that *Thomasomys* and *Aepeomys* deserved generic status as a result.

However, karyotypic differences between *Aepeomys* and *Thomasomys* were challenged by Aguilera et al. (1994), who presented a karyotype of *Aepeomys* sp. (2n = 44) very similar to those of *Thomasomys.* More recently, data on the karyotype of *T. niveipes* (2n = 24; fundamental number [FN] = 42) by Gómez-Laverde et al. (1997) put into question the hypothesis of karyologic homogeneity in *Thomasomys.*

Four species of *Thomasomys* (*T. aureus, T. hylophilus, T. laniger,* and *T. vestitus*) and 1 of *Aepeomys* (*A. lugens*) have been recorded for Venezuela (Musser and Carleton 1993; Soriano and Ochoa 1997). However, after the classical work of Gardner and Patton (1976), it became clear that species status of South American sigmodontines may be misleading without cytotaxonomic evidence. In this context, we describe karyotypes from Venezuelan specimens of *A. lugens, Aepeomys* sp., *T. vestitus,* and *T. laniger,* to have a more exhaustive diagnosis on the karyology, taxonomic status, and evolutionary patterns of this group of rodents.

Materials and Methods

Karyologic analyses were carried out on 13 specimens (8 males and 5 females) of *A. lugens* trapped at its type locality (El Morro, 9 km SSW Mérida City, Mérida State) and Páramo Los Colorados (Páramos Batallón y La Negra National Park, Táchira State). We also examined 5 specimens (4 males and 1 female), referred to as *Aepeomys* sp. (Aguilera et al. 1994), from Yacambú National Park (Lara State), 2 males and 1 female of *T. laniger* from Cerro Las Banderas, near Mérida City (Mérida State) and Páramo Los Colorados, and 1 male of *T. vestitus* from El Baho (Santo Domingo, Mérida State). Localities are indicated in Fig. 1.

Voucher specimens were deposited in the following Venezuelan collections: Colección de Vertebrados de la Universidad Simón Bolívar and Museo de la Estación Biológica de Rancho Grande. Taxonomic identifications based on external and cranial morphology were made by comparisons with specimens in those institutions and in the Colección de Vertebrados of the Universidad de Los Andes. Bone-marrow metaphase chromosomes were obtained by a modification of the Ford and Hamerton (1956) in vivo colchicine technique. The C- and G-banding patterns were obtained as described by Barros and Patton (1985) and Chiarelli et al. (1972), respectively. Chromosome nomenclature followed Levan et al. (1964). Fundamental numbers are autosomal arm numbers.

Results

Specimens of *A. lugens* from Páramo Los Colorado and those from the type locality have the same karyotype (Fig. 2), with 14 chromosome pairs (2n = 28) and 48 autosomal arms (FN = 48). Eleven pairs are biarmed chromosomes (metacentric or submetacentric), whereas 2 pairs are uniarmed chromosomes (acrocentric). The X and Y chromosomes are subtelocentric and submetacentric, respectively. The precise identification of each chromosomic pair was confirmed by the G-banding patterns (Fig. 2b). The constitutive heterochromatin (Fig. 2c) was found unequally distributed on this karyotype, with a noticeable presence in pericentromeric areas of pairs 3, 7, and 9 and the X chromosome. Short arms of pairs

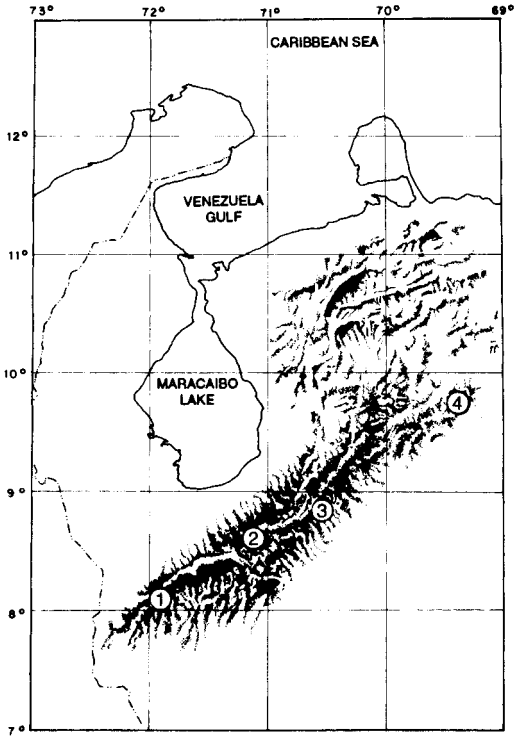

FIG. 1.—Map of western Venezuela showing sampled localities of specimens of *Aepeomys* and *Thomasomys*: 1) Páramo Los Colorados, Táchira State; 2) El Morro and Cerro Las Banderas, Mérida State; 3) Santo Domingo, Mérida State; and 4) Yacambú National Park, Lara State.

11 and 12 and the Y chromosome were fully heterochromatic, but in the remainder of the complement heterochromatin was less conspicuous.

In external and cranial features, specimens from Yacambú agree with those of *A. lugens*. However, the karyotype of this population, named here as *Aepeomys* sp., is highly differentiated from that of *A. lugens* and corresponds to that previously described by Aguilera et al. (1994) for other specimens from the same locality: 2n = 44, FN = 46 (Fig. 3). In this karyotype, the heterochromatin was conspicuous in pericentromeric areas of autosomes, whereas the short arms of the X and Y chromosomes were totally heterochromatic (Fig. 3).

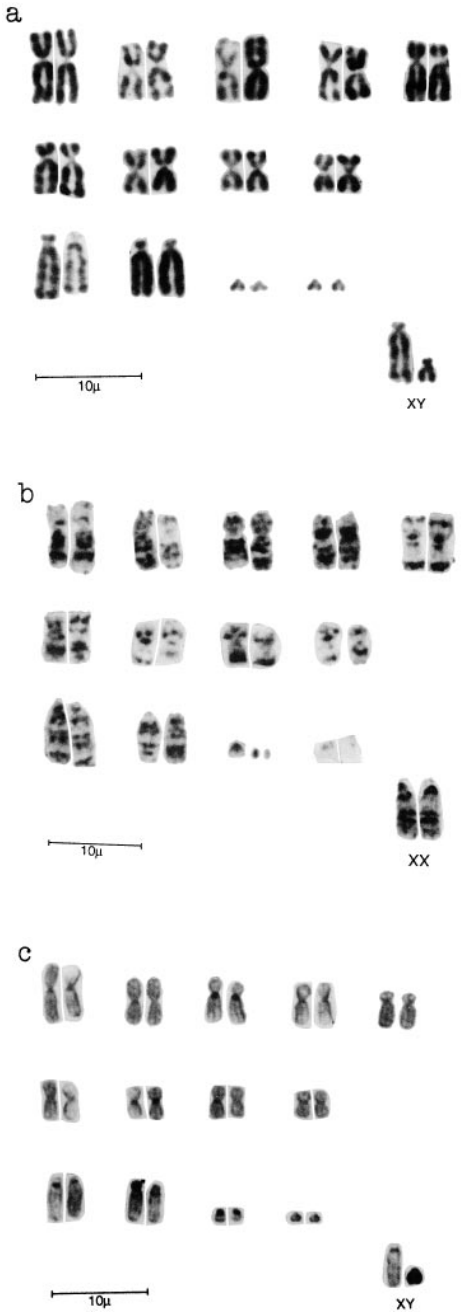

FIG. 2.—a) Giemsa-stained, b) G-banded, and c) C-banded karyotypes of *Aepeomys lugens* from the Venezuelan Andes.

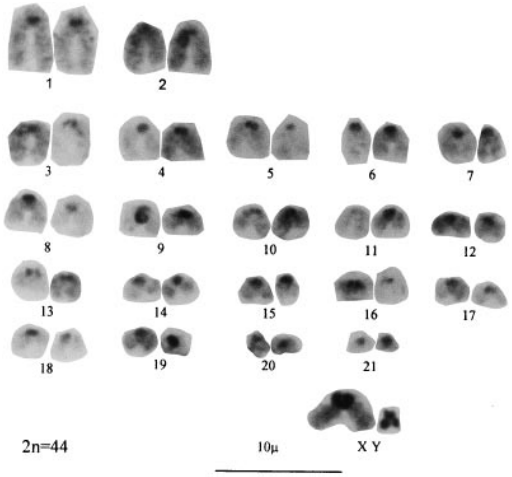

FIG. 3.—The C-banded karyotype of *Aepeomys* sp. from the Venezuelan Andes.

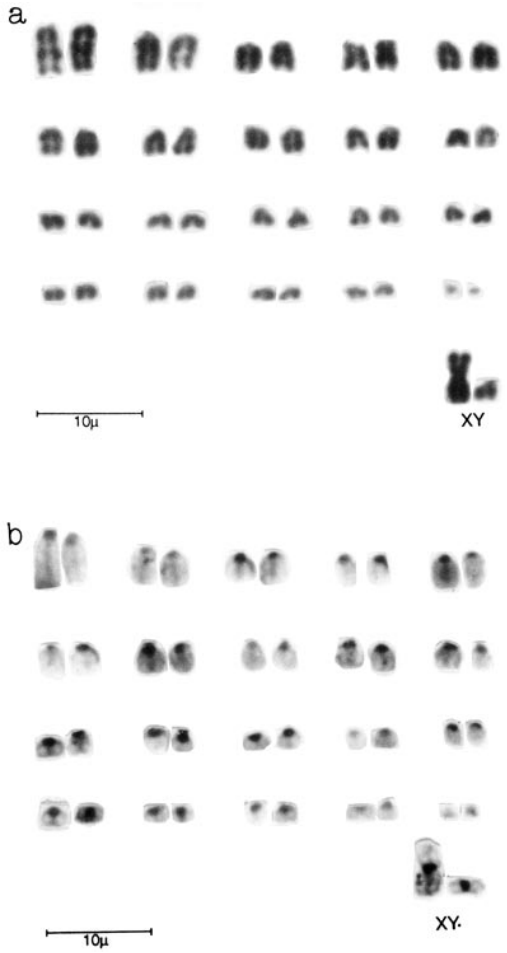

FIG. 4.—a) Giemsa-stained and b) C-banded karyotypes of *Thomasomys laniger* from the Venezuelan Andes.

Thomasomys laniger and *T. vestitus* had karyotypes of 2n = 42, FN = 40 (Fig. 4) and 2n = 44, FN = 42 (Fig. 5), respectively. In *T. laniger*, all autosomes are acrocentric, and the X and Y chromosomes are metacentric and acrocentric, respectively. The karyotype of *T. vestitus* was different from that of *T. laniger* because in the former an additional pair of small-sized metacentric chromosomes was present and the X chromosome was acrocentric. The C bands were obtained only in *T. laniger*, which had chromosomes displaying heterochromatin in the pericentromeric areas (Fig. 4b). The G bands, which were obtained only in *T. vestitus*, showed a clear pattern that allowed a precise identification of chromosome pairs (Fig. 5b).

DISCUSSION

The karyotype of *A. lugens* (Fig. 2) is reported here for the 1st time. It is characterized by a low diploid number (2n = 28) and a predominant presence of biarmed elements (FN = 48). On the other hand, *Aepeomys* sp. has a karyotype (2n = 44, FN = 46; Fig. 3) comparable with those described for the majority of *Thomasomys* species (see below). Also, the karyotypes of *Aepeomys* sp. and *A. lugens* are different from that of *A. fuscatus* (2n = 54, FN = 62) from Colombia (Gardner and Patton 1976).

Our karyologic analysis of *Aepeomys* sp. and *A. lugens*, based on the number and structure of chromosomes in addition to the available information on this genus, leads us to consider specimens from Yacambú as a differentiated population, probably a new species.

Unfortunately, we had no success in G-banding the karyotype of *Aepeomys* sp., which would have allowed an arm-to-arm comparison between the Venezuelan forms

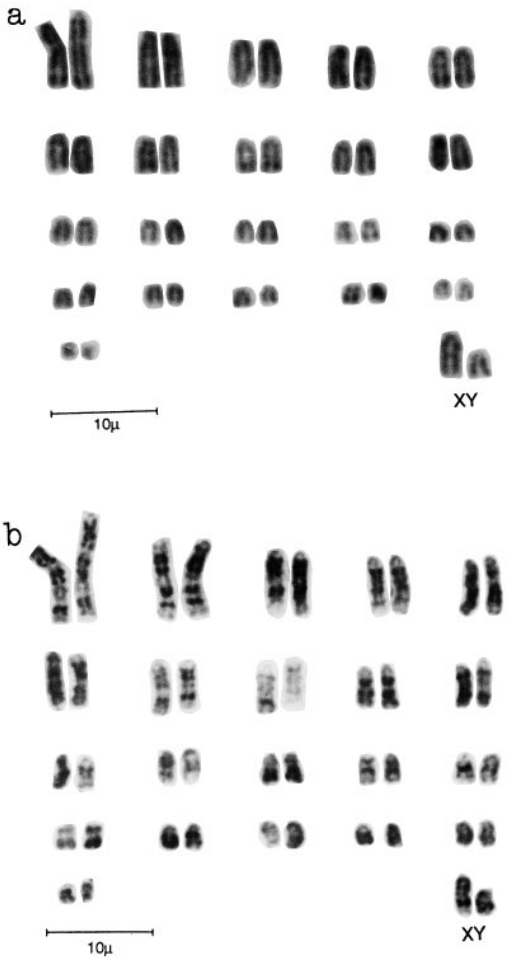

FIG. 5.—a) Giemsa-stained and b) G-banded karyotypes of *Thomasomys vestitus* from the Venezuelan Andes.

of *Aepeomys*. However, their diploid number and the similarity of their fundamental numbers (46 and 48) lead us to postulate that the differentiation of *Aepeomys* sp. may be the result of chromosomal rearrangements, mainly Robertsonian changes.

A point worth discussing is the direction of the chromosomal transformation between *Aepeomys* sp. and *A. lugens*. According to Gardner and Patton (1976), thomasomyine karyotypes are characterized by a general condition of diploid numbers of 42 or 44, in addition to a predominantly acrocentric autosomal complement, a condition shared by this group with several other oryzomyine species. The karyotype of *Aepeomys* sp. meets this general condition; for this reason, we consider it a primitive form. However, presence of a high proportion of biarmed elements in *A. lugens* suggests that this species is a derived form.

Further evidence for this hypothesis is the difference in amount and distribution of constitutive heterochromatin. In *A. lugens* this heterochromatin is present in low amounts and is restricted to a few chromosomes, but in *Aepeomys* sp., this heterochromatin is abundant and distributed in all chromosomes. This last pattern is considered a primitive condition in eukaryotic chromosomal evolution (Imai 1981). The derived condition of low-numbered karyotypes, with low amounts and restricted distributions of constitutive heterochromatin, also has been suggested for other oryzomyine species, for example *Nectomys palmipes* (2n = 16–17; Barros et al. 1992) and *Oryzomys talamancae* (2n = 34; Pérez-Zapata et al. 1996). Thus, species of *Aepeomys* are chromosomally very different. They are members of a group where the speciation process was accompanied by chromosomal reorganization.

Regarding *T. laniger*, the karyotype reported at the type locality (2n = 40, FN = 40) by Gómez-Laverde et al. (1997) has a conspicuous large submetacentric pair; this feature is uncommon among *Thomasomys* karyotypes (Gardner and Patton 1976). Results for *T. laniger* from Venezuela (2n = 42, FN = 40; Fig. 4) and Colombia indicate that at least 2 different cytotypes should be included in this species. The comparison between those cytotypes suggests that a single Robertsonian rearrangement may be involved in their differentiation.

The karyotype of *T. vestitus* (2n = 44, FN = 42; Fig. 5), described herein for the 1st time, is similar both in number and in structure to the karyotype of *T. laniger* from Venezuela. This karyotype also is similar to karyotypes reported by Gardner and Patton (1976) for several species from

Colombia, Perú, and Ecuador: *Thomasomys* sp., *T. aureus* (2n = 44, FN = 42), *T. kalinowskii, T. notatus,* and *T. taczanowskii* (2n = 44, FN = 44). It is worth noting that most of the chromosomes of *Thomasomys* are acrocentric, supposedly a primitive condition in the Sigmodontinae (Gardner and Patton 1976). These authors pointed out that the karyotypes of the thomasomyines are similar to that of *Oryzomys palustris* (2n = 56, FN = 56), which has a general formula within the South American murids. The primitive condition of karyotypes of *Thomasomys* also is indicated by the constitutive heterochromatin of *T. laniger*, which is centromeric and abundant in all autosomes (Imai 1981; Fig. 4).

Our results indicate that 2 chromosomal patterns exist in *Thomasomys*: 1 is primitive and is found in *T. aureus, T. kalinowskii, T. notatus, T. taczanowskii,* and *T. laniger*. The other, exemplified by *T. niveipes* (Gómez-Laverde et al. 1997), is characterized by a prevalence of biarmed elements resembling the karyotype of *A. lugens.* This may be considered a derived condition in the karyotypic evolution of *Thomasomys.*

Analysis of our data strongly suggests that *Aepeomys* and *Thomasomys* are closely related taxa and chromosomal reorganization may have been involved in their differentiation. Karyotypic patterns and cranial features (J. Ochoa et al., in litt.) of these 2 taxa allow us to consider them as differentiated forms at a generic level

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