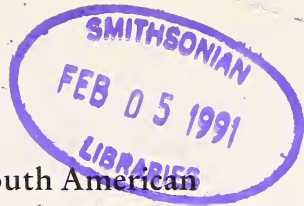


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Cytogenetics and karyosystematics of South American oryzomyine rodents (Cricetidae: Sigmodontinae)

II. High numbered karyotypes and chromosomal heterogeneity in Venezuelan *Zygodontomys*

By O. A. REIG, M. AGUILERA, and A. PEREZ-ZAPATA

GIBE, Departamento de Ciencias Biológicas, Universidad de Buenos Aires, Buenos Aires, Argentina
and Departamento de Estudios Ambientales, Universidad Simón Bolívar, Caracas, Venezuela

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Abstract

Studied karyotypes in savanna mice of *Zygodontomys microtinus thomasi* and *Z. m. stellae* from sixteen localities in Venezuela. Fifteen males and thirteen females from ten populations of the former, and three males and two females from one population of the latter showed a $2n = 84$, $FN = 116-118$ karyotype comprising mostly small bi-armed autosomes and an XY-XX sexual pair. C-banding showed that a great deal of the genome was heterochromatic, including pericentromeric, whole arm, and whole chromosome heterochromatin types. Three males and six females from one population of Monagas State (Isla Guara), which did not differ in morphology from *Z. m. thomasi*, showed a different karyotype of $2n = 88$, $FN = 116-118$ which can be derived from the former by two Robertsonian fissions. The taxonomy of *Zygodontomys* is briefly discussed.

Introduction

The chromosomes of the cricetid savanna mouse *Zygodontomys microtinus* were briefly described twenty years ago on the basis of specimens from several localities in Venezuela (KIBLISKY et al. 1970). The karyotype comprised $2n = 84$ chromosomes, at that time the highest chromosome number for a mammal, only matched by a similar diploid number previously communicated for the black rhinoceros (HUNGERFORD et al. 1967). Later on, two papers reported chromosome numbers or briefly described the karyotypes in samples of *Zygodontomys* from other localities (GARDNER and PATTON 1976; TRANIER 1976). However, neither an accurate description, nor an illustration of the chromosomes of a species of this genus has been published so far.

During the last 15 years we have obtained new information on chromosomes of Venezuelan *Zygodontomys*. The recent discovery of polytypic variation in the karyotypes of *Zygodontomys* (PEREZ-ZAPATA et al. 1984) added to our increasing interest in the biology (AGUILERA 1985), and systematics (REIG 1987) of species of this genus and induced us to present our results.

Material and methods

Forty-two specimens of *Zygodontomys* (twenty-one of each sex) are included in the present study (see specimens examined). Animals were captured by live trapping at sixteen localities covering a large portion of Venezuela (Fig. 1).

All animals processed were deposited in the collection of mammals of the Museum of Biology, Central University of Venezuela, Caracas, Venezuela (MBUCV), and the Museum of Natural Sciences of the Simón Bolívar University in Caracas (USB).



Fig. 1. Map of Venezuela showing localities of the studied specimens of *Zygodontomys*. Numbers at each marked point correspond to localities as defined in the text under "Specimens examined"

All specimens were brought alive to the laboratory for standard bone-marrow chromosome preparations (REIG et al. 1971). A few animals were also processed following FREDGA's (1964) cornea technique. C-banding was obtained in a few of them following SUMNER (1972). A few males were also processed for meiotic chromosomal preparations after PATHAK and HSU (1979). For nomenclature of chromosomes we followed LEVAN et al. (1964). For the assortment of chromosomes into size classes, we called medium-sized those between 5.5 and 9.0 % of the length of the female haploid set (LHS); small those between 2 and 5.5 %, and minute those < 2 % of the LHS. Fundamental number (FN) is the number of autosomal arms.

Specimens examined

Localities and collection numbers are as follows: 1. Barinitas, Barinas State: one male (USB K-097). 2. Tierra Buena, Portuguesa State: one male (USB K-416). 3. Turén, Portuguesa State: one female (USB K-059). 4. La Batea-Morón, Carabobo State: one female (USB K-803). 5. Manuare, Carabobo State: one male (USB K-081). 6. Calabozo, Guarico State: four males (MBUCV 1-1838; USB K-197, K-237, K-242) and six females (MBUCV 1-1839, 1-1840, 1-1841; USB K-238, K-241, K-310). 7. Hato "El Frío", Apure State: two males (USB K-441, K-480) and one female (USB K-474). 8. San José de Guanipa, Anzoátegui State: one female (USB K-796). 9. Río Pao-Hato San Antonio, Anzoátegui State: two males (USB K-654, K-657). 10. Paso Bajito-El Tigrito, Anzoátegui State: one female (USB K-645). 11. San Vicente, Sucre State: two males (USB K-691, K-693) and one female (USB K-692). 12. San Juan de las Galdonas, Sucre State: one female (USB K-670). 13. Isla Guara,

Monagas State: three males (USB K-621, K-624, K-627) and six females (USB K-617, K-620, K-622, K-636, K-637, K-638). 14. Ciudad Bolívar, Bolívar State: one male (MBUCV A-365). 15. El Guri, Bolívar State: one male (MBUCV 1-1657). 16. La Esmeralda, Amazonas Federal Territory: three males (MBUCV 1-1763, 1-1931, 1-1953) and two females (MBUCV 1-1932, 1-1954).

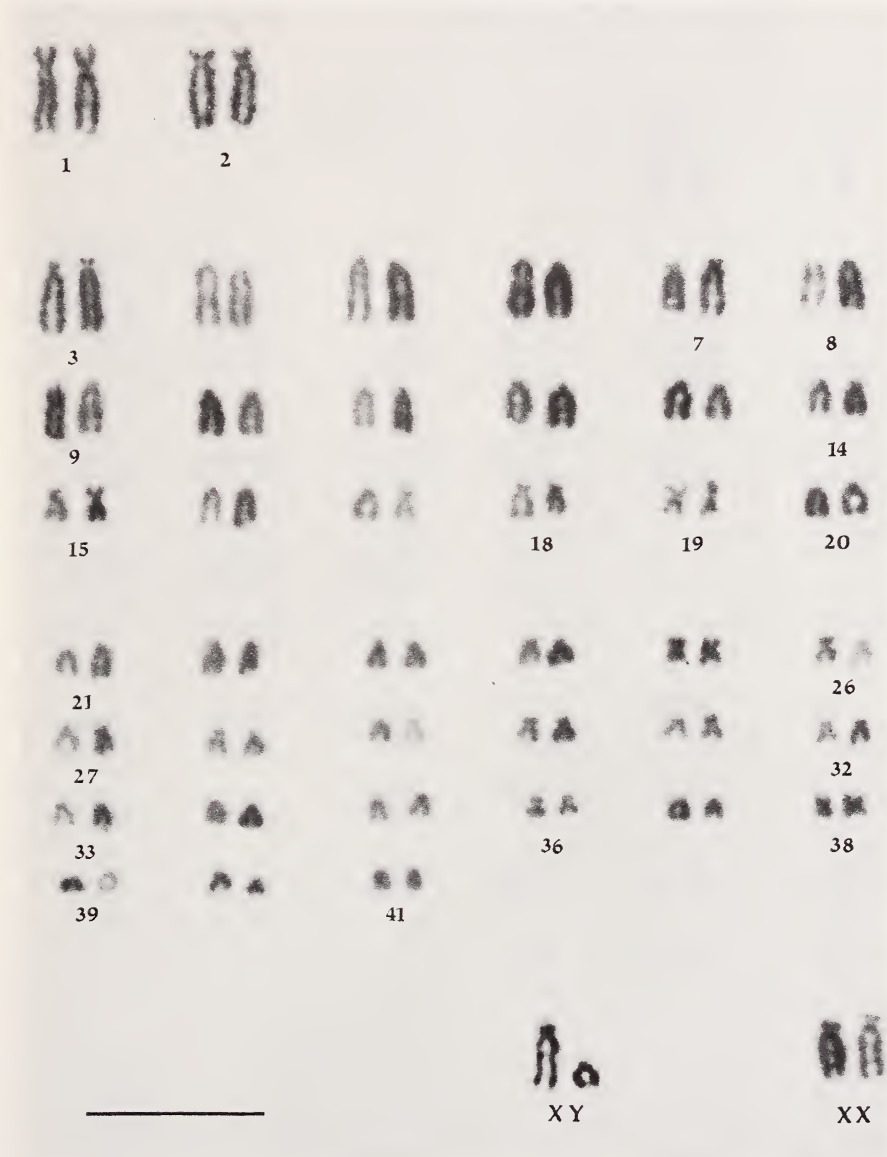


Fig. 2. Representative $2n = 84$ bone-marrow karyotype of *Zygodontomys microtinus thomasi* and *Z. m. stellae*, as shown in a female individual from Paso Bajito-El Tigrito, Anzoátegui State, Venezuela. Illustrated are also the sex chromosomes of one male from Rio Pao-Hato San Antonio in the same State. Bar represents 5 μm

Results

A karyotype of $2n = 84$ was found in all individuals examined, except those from Isla Guara (Fig. 2). This number was confirmed by 42 bivalents counted in several diakineses, and by the same number counted in meiotic II metaphases. This karyotype is composed of 41 pairs of gradually decreasing autosomes and an XY/XX gonosomal set (Fig. 2). Of the autosomes, chromosomes of pair 1 are middle-sized submetacentrics amounting to 5.8 %



Fig. 3. Representative C-banded bone-marrow karyotype of *Zygodontomys microtinus thomasi* of a female individual from Paso Bajito-El Tigrito, Anzoátegui State, Venezuela. Bar represents 5 μm

LHS, and an average of 3.8 (3.0–4.8) μm of absolute size. Those of pair 2 are subtelocentric a little smaller than the former (5.5 %). Pairs 3 to 20 are small sized autosomes gradually decreasing in size from 4.6 % to 2.0 % LHS, and pairs 21 to 41 are minute chromosomes very similar in size, which also gradually decrease from 2.0 to 1.0 % LHS. Due to the small size of most autosomes, it was hard to recognize the morphology of many of the chromosomal pairs in all individuals examined. Moreover, the heterochromatic nature of some of the short arms (see below), may be responsible for polymorphic variants in the morphology of several autosomes among different individuals. The following description is based on the best-defined karyotypes from Anzoátegui (Fig. 2). Of the small sized series made of chromosome pairs 3 to 20, pairs 3, 7 and 18 are subtelocentric and pairs 15 and 19 are submetacentric and metacentric, respectively. The remaining pairs are either telocentric or show an indication of a very small short arm. Of the 21 pairs of minute autosomes, four



Fig. 4. $2n = 88$ bone-marrow karyotype of *Zygodontomys microtinus thomasi* of a male individual from Isla Guara, Monagas State, Venezuela. Illustrated are also the sex chromosomes of one female from the same locality. Bar represents 5 μm

pairs are likely to be metacentric, and further six or seven are also clearly biarmed, whereas in the remaining pairs the presence or absence of short arms cannot be decided. Therefore, of the 41 autosomal pairs, 17 or 18 are biarmed, and 24 or 23 are likely to be telocentric chromosomes, allowing us to tentatively estimate the autosomal FN as made of 116 or 118 arms. Autosomes of pair 36 are telocentric showing a secondary constriction. The X-chromosome is a small-sized subtelocentric ($r = 3.39$) amounting 4.1 % LHS, and the Y-chromosome is a subtelocentric of minute size.

Although C-banding was not very clear in overall resolution in all treated cells and specimens, it allows us to conclude that a great deal of the genome is C-positive (Fig. 3). However, the small size of most chromosomes makes it difficult to ascertain the C-pattern of each chromosomal pair. The following description is based on a few good C-band resolutions we obtained in specimens from Anzoátegui. Chromosomes of pairs 1 and 2 lack a striking C-staining region, whereas those of pairs 3 to 7 exhibit both pericentromeric heterochromatin and a clear-cut terminal heterochromatic block. All the remaining autosome pairs show different degrees of C-staining. Those of the small-sized series exhibit in all cases a neat centromeric banding, and in addition three of them, corresponding to pairs 15, 18 and 19, have a full small arm heterochromatic block in all examined cells. Five of the minute autosomes are entirely C-positive, and the remaining sixteen pairs are C-positive in one third or more of their lengths, suggesting either large pericentromeric or full-arm blocks. The X-chromosome is C-positive only at the centromeric region, and the banding pattern of the Y-chromosome was not clearly defined.

Another slightly different karyotype was found in the nine analyzed specimens from Isle Guara. Here we have a karyotype of $2n = 88$, FN = 116–118 (Fig. 4). The difference in diploid numbers affects the set of autosomes of the minute-sized class, where the addition of two pairs of autosomes is observed. Therefore, the autosomal set of the minute-sized series of the $2n = 88$ is made of 23 pairs, instead of the 21 pairs found in the $2n = 84$ complement. Besides, the small-sized series maintains the same number of 18 pairs, but the metacentric and the submetacentric pairs found in the $2n = 84$ karyotype are lacking here. These differences can be easily explained by two Robertsonian fissions affecting pairs 15 and 19 of the $2n = 84$ karyotype. However, because of the lack of good G-band resolution confirming the arm homologies, this interpretation is merely tentative. One specimen from Isla Guara produced successful C-banding. Here again a great deal of the genome was C-positive, although the small size and high number of chromosomes hampered efforts to obtain a clear-cut banding pattern in each of the pairs. It is evident, however, that eleven pairs of minute autosomes are fully C-positive, and five pairs of the small-sized series also appear to be fully heterochromatic.

Discussion

Zygodontomys has been difficult to classify among the groups of South American cricetids, which are currently divided into seven tribes (REIG 1980). Of these, it has been more frequently grouped with the Akodontini (THOMAS 1916; ELLERMAN 1941; VORONTZOV 1959; CABRERA 1961; GARDNER and PATTON 1976), but TATE (1932) considered it to belong to the Oryzomyini, and HERSHKOVITZ (1962) argued that it must be grouped with the Phyllotini. On the grounds of its chromosomal characteristics, one of the present authors concluded that *Zygodontomys* should be removed from the Akodontini, and may represent a direct oryzomyine derivative, which because of its dubious relationships would better be placed as a Sigmodontinae *incertae sedis* (REIG 1980, 1987). We now believe that the high-numbered chromosomal complement of *Zygodontomys* is more likely to represent a primitive oryzomyine condition, as very high chromosomal numbers are more common in members of the tribe Oryzomyini than in members of the remaining tribes of the Sigmodontinae. Of the 18 species of mammals showing diploid numbers of 80 or

Mammalian species with diploid numbers equal or higher than $2N = 80$

Taxon	2n	FN	Source
RODENTIA, MYOMORPHA			
CRICETIDAE, SIGMODONTINAE			
Ichthyomyini			
<i>Chibchanomys trichotis</i>	92	102	GARDNER 1971; VOSS 1988
<i>Ichthyomys pittieri</i>	92	98	SCHMID et al. 1988
Sigmodontini			
<i>Sigmodon alstoni</i>	80–82	—	REIG 1987
Oryzomyini			
<i>Oecomys "bicolor"</i>	80	134–136	GARDNER and PATTON 1976
<i>Oecomys "concolor"</i>	80	112	GARDNER and PATTON 1976
<i>Oryzomys "albicularis"</i>	80	92	GARDNER and PATTON 1976
<i>Oryzomys nitidus</i>	80	86	GARDNER and PATTON 1976
<i>Oryzomys macconelli</i>	80	—	LEITAO and BARROS 1977
<i>Delomys dorsalis collinus</i>	82	—	YONENAGA 1975
<i>Zygodontomys brevicauda</i>	84	—	GARDNER and PATTON 1976
<i>Zygodontomys microtinus</i>	84–88	—	GARDNER and PATTON 1976
<i>Zygodontomys microtinus</i>	84	—	KIBLISKY et al. 1970
<i>Zygodontomys microtinus</i>	88	—	PEREZ-ZAPATA et al. 1984
<i>Zygodontomys microtinus</i>	84–88	116–118	This report
RODENTIA, CAVIOMORPHA			
CAPROMYIDAE			
<i>Geocapromys browni</i>	88	136	GEORGE and WEIR 1972
PERISSODACTYLA			
RHINOCEROTIDAE			
<i>Ceratotherium simum</i>	82	—	HEINICHEN 1969
<i>Diceros bicornis</i>	84	172	HUNGERFORD et al. 1967
<i>Rhinoceros unicornis</i>	82	—	WURSTER and BENIRSCHKE 1968
TAPIRIDAE			
<i>Tapirus terrestris</i>	80	—	MATTHEY 1973
PRIMATES			
TARSIIDAE			
<i>Tarsius bancanus</i>	80	94	CHIARELLI et al. 1979
<i>Tarsius syrichta</i>	80	94	CHIARELLI et al. 1979
FN = Number of autosomal arms. See under "References" for source of information.			

more chromosomes, 6 species other than the sigmodontines *Chibchanomys trichotis* (= *Anotomys leander*, see VOSS 1988), *Ichthyomys pittieri*, *Sigmodon alstoni* and those of *Zygodontomys*, are members of the tribe Oryzomyini, whereas the remaining 7 species are assorted among the Perissodactyla, Caviomorpha and Primates (Table). These data certainly support GARDNER and PATTON's (1976) conclusion that the structurally primitive group of the oryzomyines is characterized by high chromosome numbers, and that a diploid number near 70 or 80 most likely is the progenitor state for oryzomyines and South American cricetids in general (but see BAKER et al. 1983). Thus, karyological data strongly support the hypothesis that *Zygodontomys* is closely linked to the early radiation of the Oryzomyini, and is better classified within that tribe, as originally held by TATE (1932).

It is now generally agreed that the name *Zygodontomys* should be limited to the "northern group" of HERSHKOVITZ (1962) (see REIG 1987; MACEDO and MARES 1987). But there is extensive disagreement about the number of species to be recognized within that assemblage. Opinions vary from recognizing ten (TATE 1932) or four species (CABRERA 1961), to the extreme position held by HERSHKOVITZ (1962), who only recognizes one species: *Z. brevicauda*, a view that has been accepted uncritically by most later authors (see, for instance, HONACKI et al. 1982).

After a regrettably brief examination of the types and other original materials in the British Museum, one of us (OAR) concluded that the taxonomy of *Zygodontomys* is much more complex than what HERSHKOVITZ supposed. Morphological and geographical discontinuities in the material examined allowed for provisional recognition of four species and 13 subspecies: *Z. brevicauda* (including *brevicauda*, *cherriei*, *tobagi*, *soldadoensis*, *seorsus*); *Z. microtinus* (including *microtinus*, *thomasi*, *stellae*); *Z. punctulatus* (including *punctulatus*, *griseus*, *fraterculus*), and *Z. bruneus* (including *bruneus*, and *sactaemartae*). An additional probable member of *Zygodontomys* is *Oryzomys borreiroi* Hernandez (1957) (see GARDNER and PATTON 1976). As regards *Z. reigi* from the French Guiana (TRANIER 1976), the senior author, after the study of the type and original series, did not find reasons to separate those specimens from *Z. m. microtinus*, as reported by HUSSON (1978) for specimens of Surinam.

Specimens from the Venezuelan states of Guárico, Barinas, Sucre, Carabobo, Apure, Portuguesa, Bolívar, and Anzoátegui, are similar in size, fur color and morphology, and they agree with the type of *Zygodontomys microtinus thomasi* Thomas, being thereby identified as belonging to that taxon. The specimens from Isla Guara, though they differ in chromosome number, were indistinguishable from the former in overall morphology, and are thus identified as a chromosomal variant of the same taxon. The single sample from La Esmeralda clearly belongs to *Z. microtinus stellae* Thomas. Specimens of this sample differ from the former in being darker in fur color and larger in size. The fact that they belong to the same species was supported by obtaining viable laboratory hybrids from one male of the later and a female of the former (GARCIA 1970).

TRANIER (1976) based *Z. reigi*, among other characters, in the possession of $2n = 78$ instead of $2n = 84$ chromosomes. This was probably a miscount easy to occur when dealing with high chromosomal numbers, as other slides from the same locality observed by one of us (OAR) gave a normal $2n = 84$ count.

GARDNER and PATTON (1976) reported a karyotype of $2n = 84$ for *Z. brevicauda* from Costa Rica. At the same time, these authors found a karyotype of $2n = 88$ in a *Z. microtinus* from Villavicencio, Colombia. The first report can be interpreted as an indication of karyotypic stability among different species of *Zygodontomys*. The second is congruent with our discovery of karyotypic poltypy in *Z. microtinus*. However, we need better knowledge of the chromosomes of additional samples of *Zygodontomys* to further settle the question of the interspecific and intraspecific variability of karyotypic constitution in this genus. In view of the extensive occurrence in the studied karyotypes of great amounts of heterochromatin both of the pericentromeric and of the whole-arm and even whole-chromosome type, it is expected that a great amount of polymorphism and polytypism will be demonstrated when more evidence becomes available.

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Zusammenfassung

Zytogenetik und Karyosystematik bei südamerikanischen Rodentia der Gruppe Oryzomyini (Cricetidae: Sigmodontinae). II. Hohe Chromosomenzahl und Karyotyp-Heterogenität bei *Zygodontomys microtinus* in Venezuela

Die Chromosomen von 42 Mäusen der Art *Zygodontomys microtinus* von 16 Herkunftsn aus Venezuela wurden untersucht. 33 dieser Tiere aus den beiden Unterarten *O. m. thomasi* und *O. m. stellae* hatten $2n = 84$ Chromosomen und $FN = 116-118$. Die C-Banden zeigten, daß Heterochromatin, das perizentromer über ganze Chromosomen und Chromosomenarme verteilt ist, einen großen Teil des Genoms darstellt. 9 Exemplare der Herkunft Isla Guara (Monagas), die sich morphologisch nicht von *Z. m. thomasi* unterschieden, hatten $2n = 88$ Chromosomen. Ihr Karyotyp ist von dem sonst gefundenen durch zwei Robertsonsche Fissionen ableitbar. Nach Ansicht der Autoren umfaßt die Gattung *Zygodontomys* 4 Arten und gehört wahrscheinlich zu den Oryzomyini.

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Authors' addresses: OSVALDO A. REIG, GIBE, Departamento de Ciencias Biológicas, F.C.E.y N., Universidad de Buenos Aires. Pabellón II, Cuarto Piso, Ciudad Universitaria, Buenos Aires 1428, Argentina; MARISOL AGUILERA and ANTONIO PEREZ-ZAPATA, Departamento de Estudios Ambientales, Universidad Simón Bolívar, Apartado 8900, Caracas 1080-A, Venezuela

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