Revista Chilena de Historia Natural
68: 185-196, 1995

G- and C-banding karyotypes of spiny rats (*Proechimys*) of Venezuela

Cariotipos de bandas C y G de ratas espinosas (*Proechimys*) de Venezuela

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ABSTRACT

G- and C- banding karyotypes are described and compared within species of the *Proechimys* [*guairae*] superspecies (*P. poliopus*, *P. guairae*, and *P. Barinas*' sp. nov.) and with those of *P. trinitatis* and *P. canicollis*. The results grossly confirm previous proposals about the pathways of chromosomal repatterning within the *P. guairae* complex, and allow to add new rearrangements in the chromosomal transformation series from 2n=42 to 2n=62. The distinction between the 2n=62 karyomorphs of *barinas* sp. nov. and *P. trinitatis*, is strengthened by both G- and C- bands. The analysis of new material showed that previous karyotypes referred to as *P. urichi* are identical to those of *P. trinitatis*, suggesting that the former is a junior synonym of the latter. The direction of the chromosomal evolution within the subgenus Proechimys as a whole, and of the guairae-group in particular, is discussed, favoring the hypothesis of change from lower to higher chromosomal numbers by centric fissions. The distribution and variation of constitutive heterochromatin in the species studied are presented.

Key words: G- and G- bamding patterns, chromosomal evolution, spiny rats.

RESUMEN

En este trabajo se describen y se comparan los patrones de bandas G y C de los cariotipos de la superespecie *Proechimys* [*guairae*](*P. poliopus. P. guairae* y *P.Barinas* sp. nov.) y de las especies *P. trinitatis* y *P. canicollis*. Los resultados confirman en lineas generales la proposición existente sobre las transformaciones cromosómicas en el complejo *P. guairae* y permiten incluir nuevos reordenamientos cromosómicos en la derivación de 2n=42 a 2n=62. La distinción entre los cariomorfos 2n=62 de *P.Barinas* sp. nov. y de *P. trinitatis* es reforzada por ambos patrones de bandas. El análisis de nuevos ejemplares muestra que el cariotipo referido como P. urichi es idéntico al de *P. trinitatiis*, por lo que se concluye que el primero es un sinónimo reciente del último. Se discute la dirección de la evolución cromosómica dentro del subgénero Proechimys en general, y dentro del grupo guairae en particular, favoreciendo la hipótesis que postula la transformación de cariotipos con 2n bajos a cariotipos con 2n elevados a través de fisiones centroméricas. Se presenta la distribución y variación de la heterocromatina constitutiva en las especies estudiadas.

Palabras clave: patrones de bandas C y G, evolución cromosómica, ratas espinosas.

INTRODUCTION

With about 60 existing named species, caviomorph spiny-rats (genus *Proechimys*, family Echimyidae) are one of the most speciose taxon of Neotropical rodents (see review in Moojen 1948, Patton 1987). Because of their extraordinay chromosomal heterogeneity revealed by the high range of diploid numbers (2n=14-65), spiny rats have been claimed to be a case in which explosive speciation may have been triggered by chromosomal repatterning (Reig 1989).

However, cytogenetic studies on Proechimys are still on a preliminary stage, and with the exception of Proechimys (Trinomys) iheringi(Yonenaga-Yassuda et al. 1985), they are limited to the description of non differentially-stained karyotypes of about one-third of the living named species (Reig et al. 1970, Patton and Gardner 1972, Reig and Useche 1976, Petter 1978, Aguilera et al. 1979, Reig et al. 1979 a,b, 1980, Reig 1980; Gardner & Emmons, 1984). Evidence of the role of chromosomal repatterning in speciation for a group of species and semispecies referred to as the superspecies *P. guairae* from western and northwestern Venezuela has been reported.

That superspecies comprises three closely related allospecies: *P. poliopus* Osgood 1914 (2n=42, FN=76), *P. guairae* Thomas 1901 (2n=44-52, FN=72), and one still undescribed new species referred to as *P. Barinas* sp. nov. (2n=62, FN=74) (see Reig

(Recibido el 5 de Marzo de 1993; aceptado el 20 de Mayo de 1994)

1980 and Reig et al. 1980). The allospecies *P. guairae* is polytypic and comprises five subspecies or semispecies characterized by distinct stable karyomorphs: *P. guairae ochraceus* Osgood 1912 (2n=44), *P. g. Falcón* subsp. (2n=46), P. g. guairae(2n=48), *P. g. Llanos* subsp. (2n=50) and *P. g. Oriente* subsp. (2n=52) (Reig et al. 1979, Pérez-Zapata et al. 1992, this paper). With the exception of the *P. g. Oriente* subsp., all the karyomorphs of the *P.* [*guairae*] superspecies are parapatrically distributed in a contiguous range boarding the Maracaibo Lake and the mountain axis of West and Northwest of Venezuela (Fig.1). So, they conform a Rassenkreis of increasing diploid number, from *P. poliopus* (2n=42) to *P. Barinas*' sp. nov. (2n=62).

The comparisons of C- and G-banding patterns among the different *P. guairae* karyomorphs, and between *P. guairae* and two other different species from Venezuela (*P. trinitatis* and *P. canicollis*),are here presented. Evidence of the chromosomal repatterning in the Rassenkreis between 2n=42 and 2n=62 karyomorphs are shown. The distribution and variation of constitutive heterochromatin in the studied species are presented.

MATERIAL AND METHODS

At the Population Biology and Evolution Laboratory of the Universidad Simón Bolivar (USB), Caracas, Venezuela, 458 specimens of Proechimys from different localities have been studied over the past sixteen years (see Table 1). Cytogenetic analysis was performed in 92 specimens (47 males, 45 females) from 26 localities of Venezuela (see Table 1). Voucher specimens are deposited in the Mammal Collection at Universidad Simón Bolivar, Caracas, Venezuela (USB). Bone marrow metaphase chromosomes were obtained according to a modification of Ford and Hamerton's (1956) technique. C-banding patterns were obtained following the barium hydroxide Giemsa technique (Barros Patton 1985), and G-bands were obtained by digestion with tripsin (Chiarelli et al. 1972). Chromosome nomenclature followed Levan et al. (1964). Fundamental numbers (FN) are autosomal arm numbers. Regarding nomenclature and chromosome grouping, we followed our previous papers (see Reig et al. 1980). The nomenclature of superspecies, as proposed by Amadon (1966), was used.

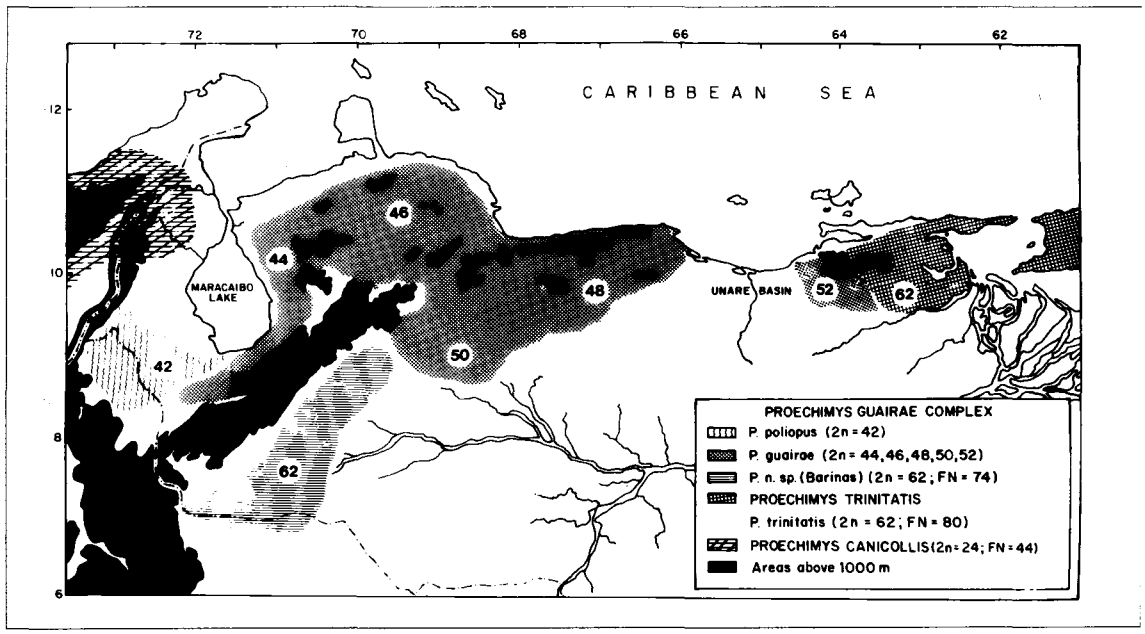

Fig. 1. Map of Northern Venezuela, showing the karyomorph distribution of the *Proechimys* [*guairae*] superspecies, *P. trinitatis* and *P. canicollis* species.

Mapa del norte de Venezuela mostrando la distribución de cariomorfos de la superespecie *Proechimys* [*guairae*], *P. trinitatis* y *P. canicollis*.

RESULTS

We obtained sharply defined G- and C-banding patterns for almost all the analysed karyomorphs, but failed to obtain a good resolution for the G-banding of *P. canicollis*.

The 2n=42, FN=76 karyotype of *P. poliopus* had four pairs in the group A of large chromosomes, eleven pairs in the group B of biarmed chromosomes and five pairs in the group C of acrocentric chromosomes (Fig. 2a). All the biarmed autosomes of A and B groups exhibited heavily stained pericentromeric C-bands. On the other hand, the distribution of constitutive heterochromatin in the uniarmed autosomes of the C group was heterogeneous; so the medium-sized chromosomes of C1 pair were negatively C-stained and the smallest C5 autosomes showed heterochromatin limited to the centromere. Autosomes of pairs C2 and C3 were strongly stained both at the centromere and at the whole extension of the arm. An interesting result was that the C4 pair was heteromorphic, showing one fully stained chromosome while the other was only

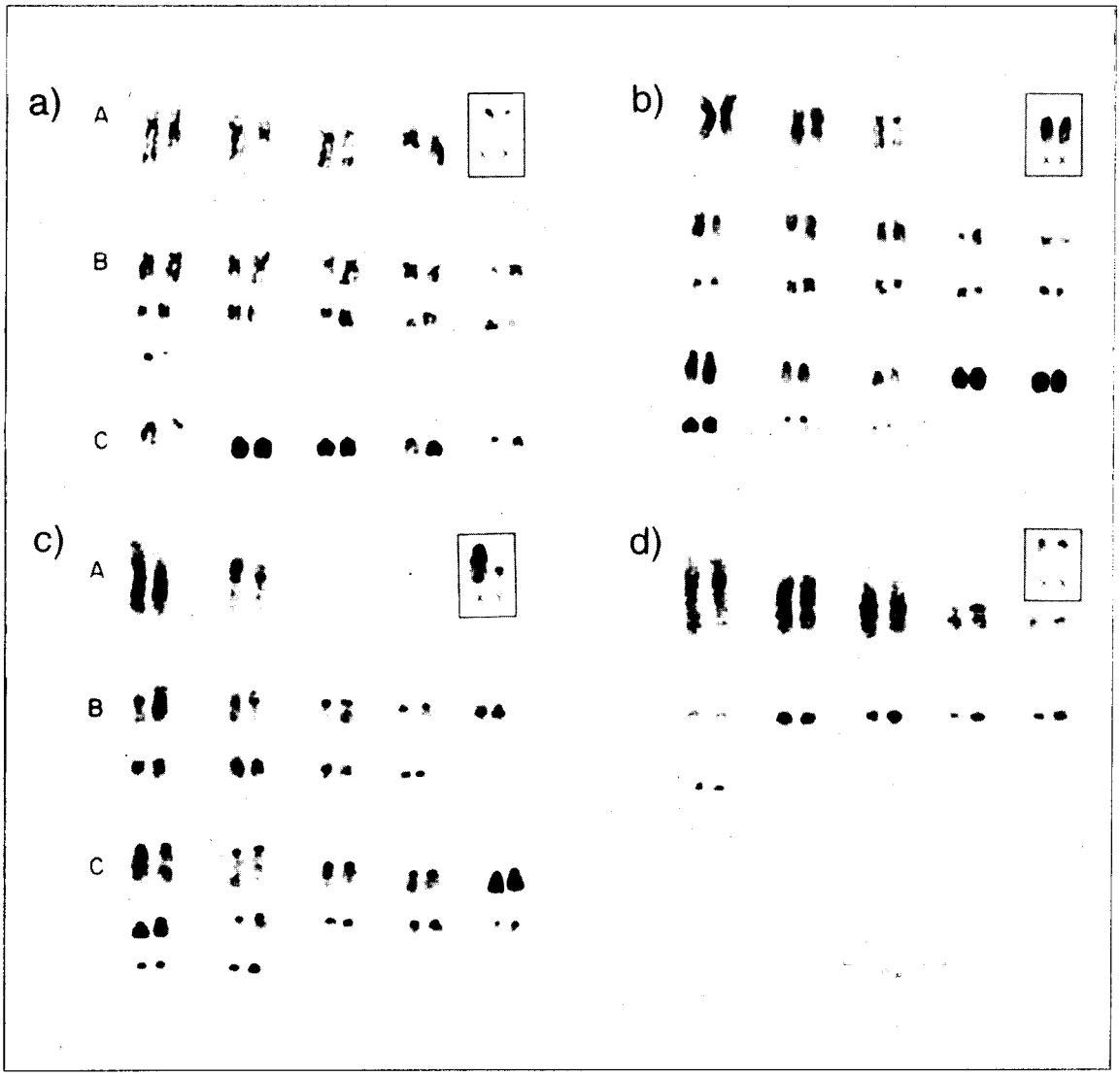

Fig. 2. C-banding karyotypes: a) *P. poliopus* (2n=42, female), b) *P. g. ochraceus* (2n=44, male), c) *P. g. guairae* (2n=48, female) of the *Proechimys* [*guairae*] complex ; d) *P. canicollis* (2n=24 , female).

Cariotipos de bandas C: a) *P. poliopus* (2n=42, hembra), b) *P. g. ochraceus* (2n=44, macho), c) *P. g. guairae* (2n=48, hembra) del complejo *Proechimys* [*guairae*], d) *P. canicollis* (2n=24 , hembra).

TABLE 1

Proechimys species and their capture localities in Venezuela (North of Orinoco river), studied in the last sixteen years at the Population Biology and Evolution Laboratory of USB. G- and C-banding was performed on specimens from localities marked with an arrow. M=male; F=female

Especies de *Proechimys* y sus localidades de captura en Venezuela (norte del río Orinoco), estudiadas en los últimos 16 años en el laboratorio de Evolución y Biología de Poblaciones de la U.S.B. El bandeo C y G fue realizado en especímenes de localidades marcadas con flechas. M=macho; F=hembra.

Species	State		Locality	Lat N - Long W	M	F	Total
P. canicollis	Zulia	→	Rio Cachirí	10°50' - 72°13'	4	13	17
2n=24							
FN=44							
P. poliopus	Mérida		Bejuquero (*,***)	08°30' - 71°42'	2	2	4
			Caño del Tigre (*)	08°25' - 71°46'	9	7	16
2n=42,44*		→	Providencia	08°55' - 71°23'	2	0	2
FN=76			Zea	08°23' - 71°48'	0	1	1
(***=sympatric 42/44)							
	Táchira		La Tendida (*)	08°30' - 71°50'	2	0	2
			San Juan de Colon	08°02' - 72°17'	2	1	3
			Umuquena	08°18' - 72°04'	1	1	2
	Zulia		El Rosario	09°07' - 72°30'			
			Kásmera	09°55' - 72°43'	6	8	14
		→	Los Angeles del Tucuco	09°48' - 72°50'	2	3	5
P. g. ochraceus	Mérida		Bejuquero (***)	08°30' - 71°42'	1	1	2
			Caja Seca	09°10' - 71°05'	1	1	2
2n=44			Las Virtudes	09°10' - 70°58'	0	1	1
FN=72		→	Río Frío	08°56' - 71°19'	2	1	3
(***=sympatric 42/44)			Río Frío Arriba	08°52' - 71°17'	4	2	6
Trujillo			Miquimboy	09°38' - 70°13'	1	1	2
Zulia			El Consejo	10°29' - 71°08'	2	0	2
			El Venado	10°04' - 70°56'	0	2	2
P. g. Falcon subsp.	Aragua		Cata	10°28' - 67°44'	2	1	3
			La Trilla	10°24' - 67°45'	8	11	19
2n=46,47+			Ocumare de la Costa	10°27' - 67°46'	1	2	3
FN=72,74**							
(***=sympatric 46/48)	Carabobo		San Esteban	10°25' - 68°01'	5	5	10
	Cojedes		La Palma (+)	09°44' - 68°32'	1	0	1
			Las Rosas (+,**)	09°48' - 68°39'	1	2	3
			Maraquita (+)	09°45' - 68°38'	1	0	1
			Solano (+,***)	09°46' - 68°37'	1	0	1
			Subida del Diablo (+,**)	09°50' - 68°39'	1	1	2
			Tierra Caliente (+,**,***)	09°50' - 68°33'	0	1	1
			Valle Hondo (+,***)	09°45' - 68°34'	0	1	1
	Falcón		Sanare	10°53' - 68°23'	1	1	2
		→	Sierra San Luis-Cabure	11°09' - 69°36'	1	0	1
		→	Sierra San Luis-Carrizalito	11°08' - 69°45'	0	1	1
	Lara	→	Bobare	10°15' - 69°29'	2	0	2
			Uveral-Bobare	10°17' - 69°32'	0	3	3
	Yaracuy		Urachiche	10°10' - 69°05'	2	2	4
P. g guairae	Aragua	→	El Consejo	10°15' - 67°16'	2	1	3
		→	El Limón	10°19' - 67°38'	9	3	12
2n=48,47+		→	Turiamo	10°27' - 67°50'	3	3	6

FN=72,74**							
(***=sympatric 48/46)	Carabobo	→	La Pascua	10°06' - 68°20'	1	2	3
			Manaure (**)	09°58' - 67°48'	1	1	2
		→	Morón (La Batea)	10°28' - 68°13'	0	3	3
	Cojedes		El Pao	09°38' - 68°08'	1	1	2
			Las Rosas (**,***)	09°48' - 68°39'	1	1	2
			Solano (**,***)	09°46' - 68°37'	1	1	2
			Subida del Diablo (**,***)	09°50' - 68°39'	1	0	1
			Tierra Caliente (+,**,***)	09°50' - 68°33'	6	3	9
	Valle Hondo		(**,***)	09°45' - 68°34'	1	2	3
	Dtto. Federal	→	Camurí Grande	10°37' - 66°43'	1	0	1
			La Sabana	10°37' - 66°23'	1	1	2
	Guárico		Dos Caminos (**)	09°35' - 67°20'	2	0	2
	Miranda		La Horqueta (Tiara)	10°09' - 67°09'	0	1	1
			San Antonio de Río Chico	10°15' - 65°57'	6	5	11
			Valle de Sartenejas	10°25' - 66°53'	1	0	1
P. g. Llanos	Cojedes		Apartaderos	09°41' - 68°56'	4	1	5
			El Baul	08°57' - 68°18'	0	2	2
2n=50,49+			El Charcoti	09°27' - 68°29'	2	0	2
FN=72			La Blanca	09°37' - 68°36'	1	2	3
(***=sympatric 50/48)			La Yaguara	09°37' - 68°35'	0	3	3
			Palmero (+,***)	09°44' - 68°34'	1	0	1
			Solano (***)	09°46' - 68°37'	1	2	3
			Tierra Caliente (+,***)	09°50' - 68°33'	1	0	1
			Valle Hondo (+)	09°45' - 68°34'	1	0	1
	Portuguesa		El Chaparro	09°08' - 69°19'	1	3	4
		→	La Trinidad	09°11' - 69°28'	17	9	26
			La Vega	09°10' - 69°26'	1	4	5
			Nueva Florida	08°57' - 69°00'	1	0	1
		→	Ospino	09°18' - 69°28'	2	5	7
			Payara	09°30' - 69°06'	1	1	2
			San Pablo	09°05' - 69°21'	3	4	7
			Turén	09°16' - 69°04'	3	3	6
P. g. Barinas subsp.	Barinas		Barinitas	08°45' - 70°25'	3	1	4
			Buena Vista	08°24' - 70°05'	0	2	2
2n=62			El Rincón	08°46' - 70°27'	2	0	2
FN=74			Guaquitas	07°27' - 71°20'	11	5	16
		→	Ticoporo		2	1	3
	Portuguesa	→	Guanare	09°04' - 69°46'	5	2	7
			La Cocuiza	09°06' - 69°38'	6	2	8
			Las Matas	09°11' - 69°35'	7	3	10
			Rio Tucupido	09°58' - 69°50'	1	1	2
			Tierra Buena	09°15' - 69°34'	14	11	25
P. g. Oriente	Anzoátegui	→	Cueva del Agua	10°10' - 64°35'	11	8	19
2n=52	Monagas	→	San Juan de Areo	09°52' - 63°53'	3	3	6
FN=74							
P. trinitatis	Monagas		Cachipo	09°55' - 63°10'	8	8	16
		→	Cueva del Guácharo	10°10' - 63°33'	7	8	15
2n=62		→	Río chiquito, Guanaguana	10°04' - 63°34'	7	5	12
FN=80							
	Sucre	→	Cumanacoa	10°15' - 63°55'	1	0	1
		→	El Algarrobo	10°40' - 62°48'	2	3	5
			El Pilar	10°33' - 63°10'	1	3	4
		→	Guaraunos	10°34' - 63°08'	1	0	1
		→	San Vicente	10°14' - 63°10'	0	1	1
		→	Santa Maria de Cariaco	10°17' - 63°35'	5	3	8
		→	Turimiquire	10°08' - 63°55'	2	0	2
TOTAL					245	213	458

stained at the pericentromeric region. This pattern was consistent in all metaphase preparations of all the specimens studied. The X chromosome was a medium-sized subtelocentric chromosome bearing a centromeric C-positive band, and the Y chromosome was a small acrocentric C-stained only at the centromere. We referred the description of the remaining karyotypes of the *P. guairae* complex (2n=44 to 2n=62) to the karyotype of 2n=42.

The 2n=44, FN=72 karyotype of *P. g. ochraceus* differed from the 2n=42, FN=76 karyotype of the *P. poliopus* just described, in that it bears one pair less in group A chromosomes, one pair less in group B chromosomes and three additional pairs in group C autosomes. Here again, the heterochromatin was homogeneously distributed at the pericentromeric region of the biarmed chromosomes of A and B groups, and heterogeneously distributed in the acrocentric group. In this last group, three pairs of fully heavily heterochromatic chromosomes, corresponding to pairs C2, C3 and C4 of *P. poliopus* were also found. In this case, however, the last pair was C-positive in the two chromosomes (Fig.2b).

The 2n=46, FN=72 karyotype of P. g. Falcon's sp. differed from that of *P. poliopus* in bearing two pairs less in group A, one pair less in group B and five additional pairs in group C chromosomes. Heterochomatin was localized at the pericentromeric region of all the biarmed chromosomes while in the C group five entirely heterochromatic chromosomes, were found as was the case of the 2n=42 karyomorph (Fig. 3a).

The 2n=48, FN=72 karyotype of *P. g. guairae* differed from the 2n=42 karyotype by two pairs less in group A, two pairs less in group B and seven additional pairs 1 in group C chromosomes. In this last group, we found only two pair of fully C-stained chromosomes (Fig. 2c).

In the 2n=50, FN=72 karyotype of *P. g. Llanos* subsp. two pairs less in group A, three pairs less in group B and nine additional pairs in the C group of autosomes

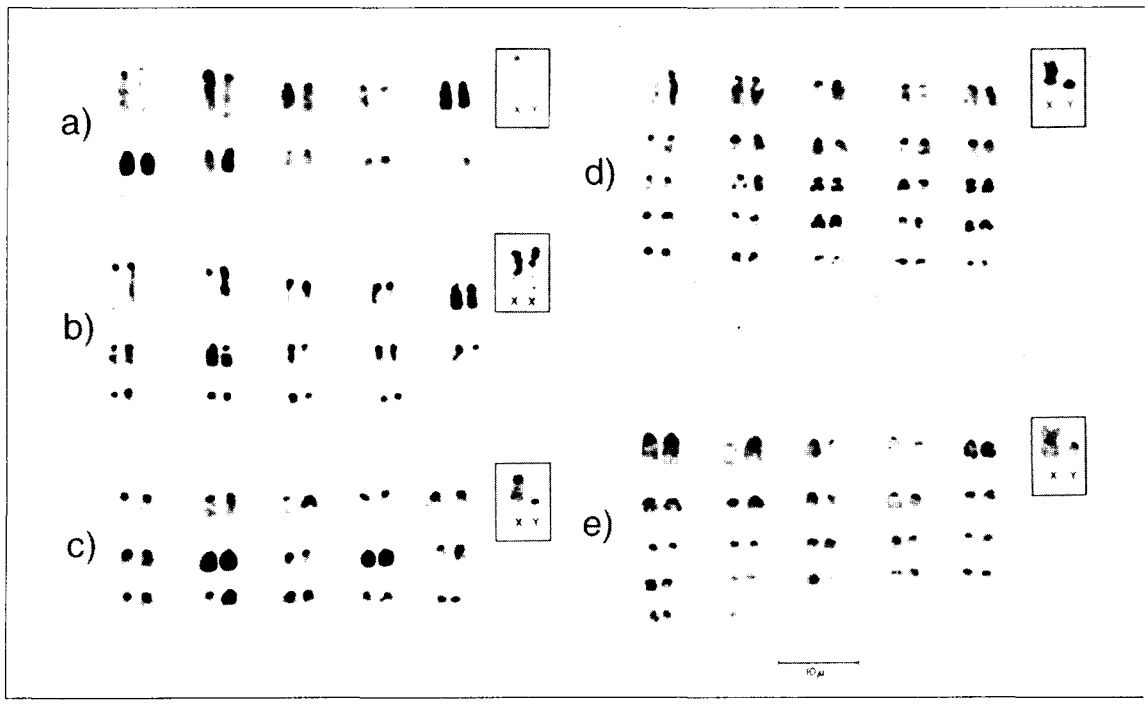

Fig. 3. C- banding patterns of the C group chromosomes of the *P.* [*guairae*] superspecies and *P.trinitatis* : a) *P. g.* Falcon subsp.(2n=46, male), b) *P. g.* Llanos subsp . (2n=50, female), c) *P. g.* Oriente subsp. (2n=52, male), d) *P. Barinas* sp. nov. (2n=62, male), and e) *P. trinitatis* (2n=62, male).

Patrones de bandas C de los cromosomas del grupo C de la superespecie *P.* [*guairae*] y de *P.trinitatis* : a) *P. g.* Falcon subsp.(2n=46, macho), b) *P. g.* Llanos subsp . (2n=50, hembra), c) *P. g.* Oriente subsp. (2n=52, macho), d) *P. Barinas* sp. nov. (2n=62, macho), y e) *P. trinitatis* (2n=62, macho).

were found in comparison whith the 2n=42 karyotype. In the acrocentric chromosomes we found two pairs of totally heterochromatic chromosomes (Fig. 3b).

The allopatric population of 2n=52, FN=72 corresponding to *P.g. Oriente* subsp. presented a karyotype which differed from the 2n=42 karyotype in that it bears three pairs less in group A, two pairs less in group B and ten pairs more in the group C of autosomes. In this last group, the condition of the fully heterochromatic chromosomes was the same as in the 2n=42 karryotype (Fig. 3c).

The 2n=62, FN=74 karyotype of *P. Barinas* sp. nov. differed radically from the 2n=42 karyotype, because it beared two pairs less in group A, nine pairs less in group B and twenty additional pairs in the group of autosomes. In the group of acrocentric chromosomes we found three pairs of entirely heterochromatic chromosomes. This karyotype was the only one of the *Proechimys* [*guairae*] complex that presented differences in the morphology of the X chromosome since it was metacentric (Fig. 3d).

The karyotype of *P. trinitatis* (2n=62, FN=80) was identical to that described by Reig et al. (1979) for this species. It is was characterized by two pairs in group A, six pairs in group B and twenty-two pairs in group C autosomes. The X chromosome was a medium-sized metacentric one, and the Y chromosome was a very small acrocentric. The C-banding pattern showed the heterochromatin localized only at the pericentromeric region of all the A and B groups (not showed), and in the sexual pair (Fig. 3e). Most in group C was C-positive only at the centromere, but there were some chromosomes weakly C-stained. Furthermore, the first pair of this group had a heavily stained region at the proximal portion (Fig. 3e).

The single specimen of *P. canicollis* studied here had a 2n=24, FN=44 karyotype which fully agrees with our previous description (Aguilera et al. 1979), . This karyotype was noticeably asymmetrical (Fig. 2d). The eleven pairs of autosomes were metacentric (only groups A and B were present). The first two pairs showed a positively C-stained band at the centromere, and a single additional band at the pericentromeric region. The third pair of group A were weakly stained at the centromeric region. The remaining pairs in group A, as well as the first pair of group B, had only faintly stained centromeric C-bands, whereas the other chromosomes in group B bore a heavily stained pericentromeric block. The telocentric medium-sized X chromosome was also well stained at the pericentromeric region (Fig. 2d).

The sharply defined distinct G-banding patterns obtained, allowed us to determine, with reasonable accuracy, the chromosomic band homology of the karyotypes, by arm-to-arm pairwise comparisons (Fig. 4). These comparisons showed that almost all the autosomal chromosomes of *P. poliopus*, were present in the remaining karyotypes of the *Proechimys* [*guairae*] complex : either in the form of intact chromosomes, or as separated arms. Indeed, some of them (26 autosomal pairs) were also identified in *P. trinitatis*. Only two exceptions were found, these involved the B3 and C5 pairs of *P. poliopus* (Fig 4b and 4c) which were affected by a pericentric inversion in the former and by a deletion in the latter. Another pericentric inversion affecting the A3 pair in the 2n=62 karyotype of P. Barinas sp. nov. (Fig. 4 a) was detected. The banding pattern of the sexual pair (Fig. 4c) was identical in all the members of the *Proechimys* [*guairae*] complex, with the exception of the X chromosome of P. Barinas sp. nov. which was affected by an inversion. This condition was also found in *P. trinitatis*.

DISCUSSION

The results confirm the diploid and fundamental numbers previously described for *P. canicollis* (Aguilera et al. 1979), and *P. trinitatis* (Reig et al. 1979) and the different karyomorphs of the superspecies *Proechimys* [*guairae*] (Reig 1980, Reig et al. 1980, Pérez-Zapata et al. 1992). They corroborate the pattern of chromosomal rearrangements within the Rassenkreis, and between it and the allopatric *P. g. Oriente*

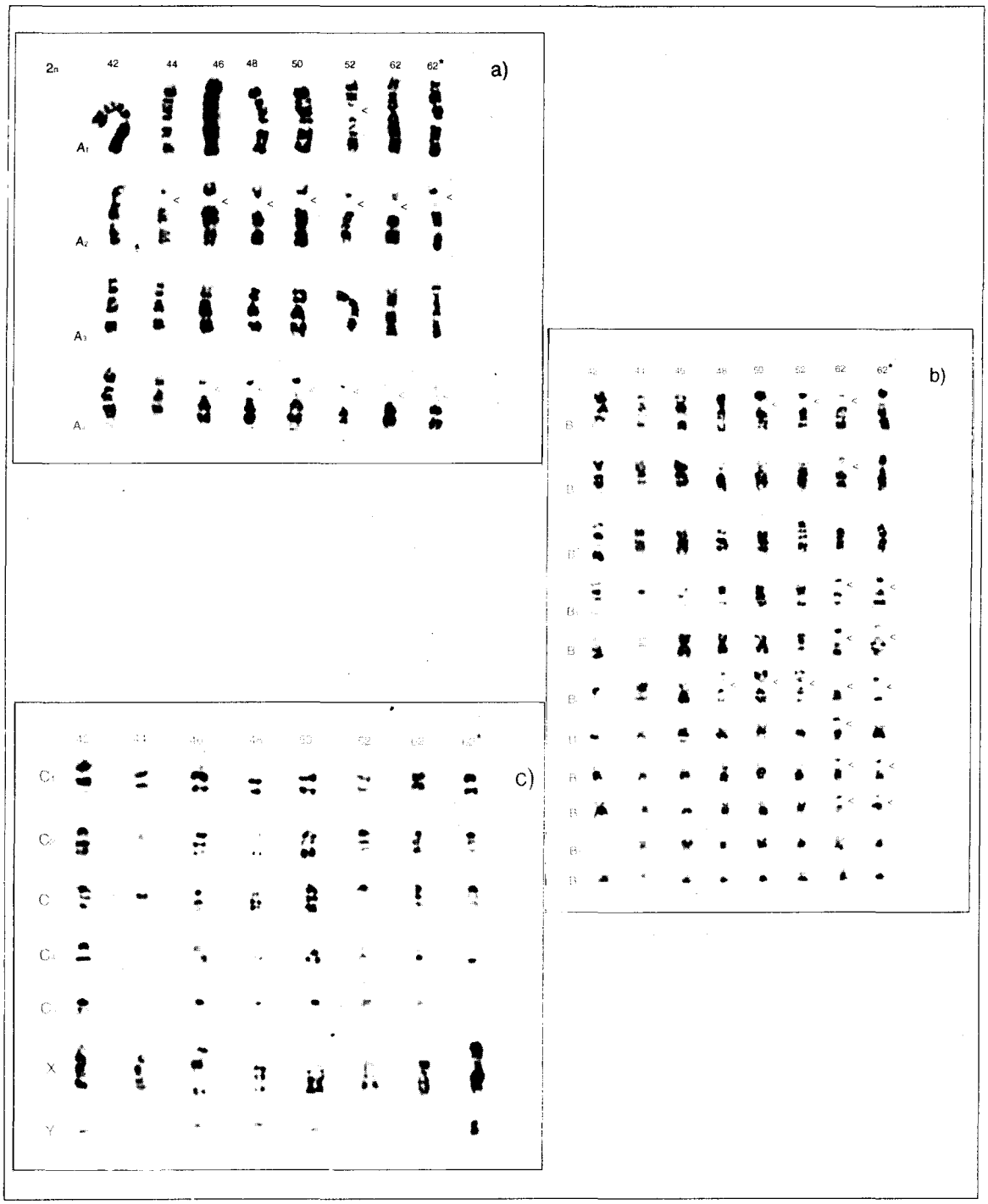

Fig. 4. G-banding patterns of karyomorphs 2n=42 (*P. poliopus*) and their homologous counterparts 2n=44, 46, 48, 50, 52, 62 (*P.* [*guairae*] superspecies) and 62 (*P.tinitatis*). a) Chromosomes in group A, b) chromosomes in group B and c) chromosomes in group C and sex chromosomes. The letters on the left identify the chromosomes of *P. poliopus*. The symbol "<" indicates the chromosomal location of a postulated rupture (Robertsonian change).

Patrones de bandas C de cariomorfos 2n=42 (*P. poliopus*) y sus contrapartes homólogas 2n=44, 46, 48, 50, 52, 62 (superespecie *P.* [*guairae*]) y 62 (*P.tinitatis*). a) Cromosomas en grupo A; b) cromosomas en grupo B and c) cromosomas en grupo C y cromosomas sexuales. Las letras a la izquierda identifican cromosomas de *P. poliopus*. El símbolo "<" indica la localización cromosómica de una ruptura postulada (cambio Robertsoniano)

subsp. previously postulated. Nevertheless, the banding results oblige us to change in part our earlier interpretation of the karyotype evolution in the *Proechimys* [*guairae*] complex. We identiffied both the nature of the chromosomal rearrangement and the chromosome involved in each transformation with more precision (Fig. 5). These results do not add new evidence regarding our previous interpretation on systematic and speciational process within the group.

In our earlier interpretation, one Robertsonian rearrangement and two pericentric inversions would explain the transformation of the 2n=42 into the 2n=44 karyotype. Banding homology demonstrates now that one Robertsonian change in pair A2, one pericentric inversion affecting pair A3, and one deletion involving pair C5 are actually present. Additionally, the data show that the two karyomorphs are sympatric in one locality south of the Maracaibo Lake (see Table 1), thus confirming our previous proposal of the full species differentiation between *P. poliopus* and *P. g. ochraceous*. It is important to point out that Zambrano (1983) found a polymorphic variant in *P. poliopus* caused by a Robertsonian change involving the B6 pair, which is represented in the variant by two additional group C telocentric autosomes. This 2n=44, FN=76 is presented as a polymorphism in three localities south of the Maracaibo Lake (Table 1). These results were obtained by non differentially-stained karyotypes.

The transformation series between 2n=44 and 2n=46, 2n=46 and 2n=48, 2n=48 and 2n=50, involves the Robertsonian changes of pairs A4, B6 and B1 respectively. The differences between the 2n=62 karyotype of P. Barinas sp. nov. and the 2n=50 karyotype are five Robertsonian changes affecting pairs B4, B5, B7, B8 and B9, one paracentric inversion on pair A3, and two pericentric inversions which involve pairs C5 and the X chromosome (Fig. 5).

Our results also confirm that the allopatric *Proechimys* populations which inhabit Eastern Venezuela described by Pérez-Zapata et al. (1992) also belong to the *Proechimys* [*guairae*]complex. This karyomorph differs from the 2n=50 karyomorph by one Robertsonian rearrangement involving the A1 pair and one pericentromeric inversion affecting the C5 pair. This last inversion is shared with the 2n=62 karyomorph of *P. Barinas* sp. nov. (Fig. 5).

C-banding reveals a relatively permanent pattern of heterochromatin distribution within the *Proechimys* [*guairae*] complex. Pericentromeric and full arm C-positive blocks are present in the corresponding shared arms of all the karyomorphs of this species complex (Figs. 2, 3 and 5). However, heterochromatin distribution varies within the *Proechimys* [*guairae*] superspecies, affecting specially the C-group telocentric chromosomes. So, we find two fully heterochromatic pairs in the 2n=48 and 2n=50 karyotipes. In the other karyomorphs (2n=42, 2n=44, 2n=46, 2n=52 and 2n=62), three heterochromatic pairs are present and one of these pairs is heteromorphic in the 2n=42, 2n=46 and 2n=52 karyomorphs. Fully heterochromatic autosomes are absent in the *P. trinitatis* karyotype, which shows C-positive bands only at the centromeric region of all the C-group autosomes and at the telomeric region of two pairs of these chromosomes. Thus, C-banding additionally demonstrates that the two karyomorphs with 2n=62, of *P. Barinas* sp. nov. and *P. trinitatis*, strongly differ in spite of sharing the same diploid number, several homologies in G-banding, and derived submetacentric X chromosomes. On the other hand, *P. canicollis* contrasts with all the other karyomorphs, since C-positive bands are scarce and limited to the pericentromeric regions (Fig. 3d).

For many years, it was believed that highly repeated heterochromatic DNA sequences were functionless and evolutionarily neutral. This view has changed lately, as evidence strongly suggests an important role of heterochromatin in the organization and evolution of chromosomes (Holmquist 1989, Pardue and Hennig 1990, Ronne 1990). It is noteworthy, therefore, to have found that heterochromatin distribution has great similarities within the *Proechimys* [guairae] complex. This homogeneous

pattern, however, is not found in the other two studied species (*P. canicollis* and *P. trinitatis*). This suggests the need to explore the pattern, composition and behavior of heterochromatin in spiny rats and its connection with the chromosomal evolution of this group, with more accurate techniques,

A further question is the direction to which chromosomal change occurs within the species studied. Different alternatives were widely discussed previously (Reig et al. 1980, Reig 1980). The hypothesis of speciation via centric fission from low diploid numbers to high diploid numbers was favored.

According to the cranial and bacular morphology study of Patton (1987), *P. poliopus*, *P. guairae*, *P. Barinas* sp. nov., and *P. trinitatis* belong to the *P. trinitatis* species group, to which *P. mincae, P. magdalenae, P. chryseolus* and *P. hoplomyoides* also belong. Of this species group, only the non differentially-stained karyotype (2n=48, FN=68) of *P.mincae* (Gardner & Emmons 1984) is known. This karyotype seems to share the four autosomal pairs in group A, and the telocentric morphology of the X-chromosome with *P. poliopus*. This can be interpreted as an indication that these cytogenetic characteristics are the primitive conditions for the *Proechimys* [*guairae*] superspecies. However, this conclusion is merely tentative, in so far as we do not know the karyotypes of the remaining species of the *trinitatis* group. On the other hand, the karyotypes of other species of the subgenus *Proechimys*, show that most of them, have low numbered chomosomal sets ranging from 2n=14 to 2n=32 (Barros, 1978, Gardner & Emmons 1984) and telocentric or subtelocentric X-chromosomes. Thus, this evidence suggest that the direction of chromosomal evolution appears to be from lower to higher numbers, and from telocentric to metacentric X-chromosomes in the subgenus *Proechimys*. It would be of interest to examine if this conclusion is bolstered by other related genera of the Echimyidae.

Proechimys belong to the subfamily Eumysopyinae (Patton and Reig, 1989), and it is probably the sister group of *Trichomys*, known in the fossil record since the early upper Miocene (Reig, 1989). The eumysopine karyotypes of *Euryzygomatomys guiara* (2n=46), *Cliomys laticeps*

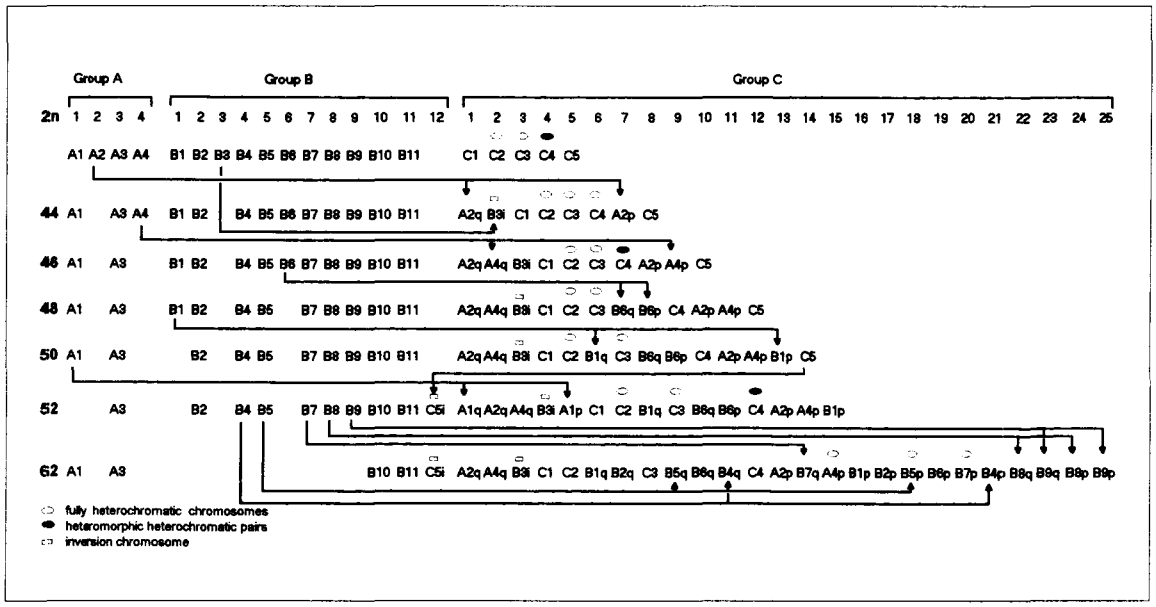

Fig. 5. Diagram of the probable transformation series of the *P.* [*guairae*] complex karyomorphs on the basis of G- and C- banding homologies.

Diagrama de la probable serie de transformación de los cariomorfos del complejo *P.* [*guairae*] sobre la base de las homologías de bandas C y G.

(2n=34, FN=60), and *Trichomys apereoides* (2n=30, FN=54), are known and have a telocentric X-chromosome (Yonenaga 1975, Souza and Yonenaga-Yassuda 1982, 1984). These eumysopine chromosomal data data also reinforce the model of chromosomal evolution within *Proechimys* [*guairae*] superspecies as postulated by Reig (1980); he considered the process of chromosomal differentiation from 2n=42 to increasing diploid numbers. However, we need chromosomal banding results from the Colombian species of the trinitatis group, to have a wide scenario of the pattern and direction of chromosomal evolution within the whole group.

Finally, our new data modify our previous view that *P. urichi* (Allen 1899) showed a karyotype (Reig & Useche 1976) different from that of *P. trinitatis* (Allen and Chapman 1893), as described by Reig et al. (1979). New better standard and banding karyotypes from Cueva del Guácharo demonstrates that the karyotypic differences reported between these two forms were due to the non resolution of short arms in small subtelocentric autosomes in our previous sample. This new conclusion is consistent with population genetic results obtained by Pérez-Zapata et al. (1992), who found no significant Nei's genetic distance between *P. trinitatis* and a population refered to as *P. urichi*.

ACKNOWLEDGMENTS

We are grateful to Angela Martino for her assistance in the laboratory work, and to José Ochoa G. for kindly providing some of the specimens included in this study. Marysolé Rondón and Arnaldo Ferrer helped in the field work. This investigation was supported by grant S1-1274 from Consejo Nacional de Investigaciones Científicas y Tecnológicas de Venezuela (CONICIT) to O. A. Reig and M. Aguilera, and by a grant from Decanato de Investigaciones Científicas-USB to M. Aguilera. We thank the Instituto Nacional de Parques (INPARQUES) for facilitating the infrastructure in the Nacional Park "Cueva del Guácharo".

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