Genetica Vol. 50, 2: 89-97, 1979

BIOCHEMICAL GENETICS OF CHROMOSOME FORMS OF VENEZUELAN SPINY RATS OF THE PROECHIMYS GUAIRAE AND PROECHIMYS TRINITATIS SUPERSPECIES

M. BENADO[1], M. AGUILERA[1], O.A. REIG[1] & F.J. AYALA[2]

[1] Departamento de Estudios Ambientales, Universidad Simón Bolívar. P.O. Box 80659. Caracas 108, Venezuela
[2] Department of Genetics, University of California, Davis, California 95616, USA

Received January 3, 1979/Accepted January 18, 1979

Spiny rats from Venezuela show an extensive karyotypic diversification (2n = 24 to 2n = 62) and little morphological differentiation. This study reports genetic distance, heterozygosity and polymorphism based upon 22 loci in semispecies and allospecies of the *Proechimys guairae* superspecies from N Central Venezuela, as compared with *Proechimys urichi*, a member of the *Proechimys trinitatis* superspecies from eastern Venezuela. Four chromosome forms of the *P. guairae* complex are included, each characterized by karyotypes of 2n = 46 (Fundamental Number = 72), 2n = 48 (FN = 72), 2n = 50 (FN = 72) and 2n = 62 (FN = 74). *Proechimys urichi* has a distinctive karyotype of 2n = 62 (FN = 88). The overall mean value of Nei's genetic identity index for all pair-wise comparisons is I = 0.942 ± 0.011. Mean identity within the *P. guairae* complex is $\bar{I}$ = 0.969 ± 0.033. Mean identity between *P. urichi* and members of that complex is $\bar{I}$ = 0.889 ± 0.011. Within the *P. guairae* complex, increased genetic divergence is correlated with higher karyotypic divergence. Heterozygosity varies from H = 0.059 to H = 0.153, with a mean value of $\bar{H}$ = 0.088 ± 0.014. The mean percent of polymorphic loci is $\bar{P}$ = 18.2 ± 3.9 after the '0,95%' polymorphism criterion, and $\bar{P}$ = 20,5 ± 5.2 after the '0.99%' criterion. These results are compared with similar data from fossorial and non-fossorial rodents. Spiny rats are non-fossorial, forest-dwelling rodents which have undergone a speciation process with little genetic divergence and extensive chromosome rearrangements.

Introduction

Spiny rats of the genus *Proechimys* are common rodents of the lowland and premontane tropical forests of Venezuela. With the exception of *P. guyannensis* (= *P. cherriei*, Reig, Tranier & Barros, 1979), and *P. canicollis* (Aguilera et al. 1979) most of the species of Venezuelan spiny rats are so similar morphologically that many of them have recently been incorrectly assigned to a single species, *P. semispinosus* (Handley, 1976).

Previous studies (Reig, Kiblisky & Löbig, 1970; Reig & Useche, 1976) have shown that there is a wide range of chromosomal diversification in *Proechimys* spiny rats, chromosome numbers varying from 2n = 24 to 2n = 62. More recent studies (Reig et al. 1978, 1979a, 1979b) suggests that three species groups can be distinguished among Venezuelan spiny rats of the genus *Proechimys* occurring N of the Orinoco River. The first group herein called the *P. guairae* superspecies, lives in N central and N W Venezuela, inhabiting both sides of the Andes and the central section of the Cordillera de la Costa (Fig. 1). This species complex comprises at least three sibling species, *P. poliopus* (2n = 42), *P. guairae* (2n = 44-50), and *P.n. sp.* (2n = 62, FN = 74). The second group, is represented by *P. trinitatis* and *P. urichi*, and these species occur in eastern Venezuela and on Trinidad. Morphologically, this group has been supposed to be so similar to the former one that its members have been regarded as conspecifics. However, there are very distinctive karyotypic differences between this group (2n = 62) and those of the *P. guairae* superspecies (2n = 42-62), which include different chromosomal

morphology and fundamental numbers (Reig et al., in prep.). The third group is represented by *P. canicollis* (2n = 24), which may belong to a Peruvian-Colombian group of species.

The purpose of this study is to assess the biochemical genetic differentiation that exists among the karyomorphs of the *P. guairae* superspecies, and to compare these data with a representative of the chromosomally different, but morphologically similar *P. trinitatis* superspecies, i.e., *P. urichi*.

Material and methods

Animals were trapped in 1976 and 1977 and transported alive to the laboratory. Blood plasma, red cells and internal organs (kidney, heart, liver, striated muscle) were preserved at –80°C. Most of the rodents were killed several days after their removal from the field. Others were kept alive from two to four weeks before processing. In August, 1977, all the samples were air-mailed to Davis, California, where final processing and the electrophoretic runs were performed.

Horizontal starch gel electrophoresis was used to separate the soluble proteins. Biochemical procedures and recipes are essentially those of Ayala et al. (1972) and Selander et al. (1971) and will be reported in full elsewhere. Gel patterns were scored by a 'blind procedure', where karyotypic morph of the sample was unknown to the scorer.

The following proteins were scored in the 106 individuals processed. It is assumed that a gene locus is responsible for each zone of electrophoretic activity.
a) Enzymatic proteins: adenylate kynase (Adkin), alcohol dehydrogenase (Adh), aldolase (Aldo), alpha-glycerophosphate dehydrogenase (αGpdh), galactose six-phosphate dehydrogenase (Gal), glucose six-phosphate dehydrogenase (G-6pdh), glutamic oxaloacetic transaminase (Got), isocitrate dehydrogenase (Idh), lactate dehydrogenase (Ldh), leucineaminopeptidase (Lap), mannose phosphate isomerase (Mpi), NADH diaphorase (Nadh-dia), phosphoglucoisomerase (Pgi), phosphoglucomutase (Pgm), six-phosphogluconate dehydrogenase (6-pgdh), tetrazolium oxidase (To), and xanthic dehydrogenase (Xdh).
b) Non enzymatic proteins: hemoglobin (Hb), 'general stain' protein (Prot).

Genetic nomenclature is as follows: loci are numbered sequentially according to the distance migrated in the gel, starting with the least anodal one; alleles are given letters in alphabetical order, starting with the one that migrated the least. Proteins that migrated cathodally are given an asterisk.

Results

The populations sampled cover a rather extensive area in north-central, north-eastern and north-western Venezuela (Fig. 1). The diploid complement and fundamental number of each are listed in Table 1. La Trilla (T), Aragua, and San Esteban (E), Carabobo, are considered two populations of the same species with 2n = 46 of the *P. guairae* complex. San Antonio (A), Miranda, with 2n = 48, San Carlos (C), Cojedes, with 2n = 50, and Barinitas (B), Barinas, with 2n = 62, are all distinct karyomorphs of the *P. guairae* superspecies. Guácharo (G), Monagas, although having the same chromosome number as Barinitas (2n = 62), is regarded as a different species (*P. urichi*) not included in *P. guairae*, attending to its geographical distribution and fundamental number. *P. guairae* together with *P. g. ochraceus* (O) (2n = 44) and *P. poliopus* (P) (2n = 42) form a 'Rassenkreis' in NW Venezuela (Reig et al., 1978, 1979) (Fig. 1). Biochemical data are not available at the present for *P. g. ochraceus* and *P. poliopus*, but they are included here for the sake of completeness.

Eleven of the 22 loci scored showed no variation; these were *Adh, Aldo, Got, Idh, Ldh-1, Ldh-2, Nadh-dia, Pgi, Pgm, Prot-1*, and *Prot-4*. The allelic frequencies of the eleven variable loci are given in Table 2. The following remarks are pertinent:
(1) No population is fixed for all loci studied.
(2) The most common allele for a given locus in a

Table 1

Diploid complements (2n) and fundamental numbers (FN) of six populations of *Proechimys*

Population	2n	FN
Proechimys guairae complex		
La Trilla (T)	46	72
San Esteban (E)	46	72
San Antonio (A)	48	72
San Carlos (C)	50	72
Barinitas (B)	62	74
P. urichi		
Guácharo	62	88

particular population is the most common one in all of them, except *Hb* and *Lap*. *To* and *Xdh* have a different most common allele in *P. urichi*.

(3) Among variable loci, *Lap* is the only one which shows variation in all populations.

Intrapopulational genetic variation is measured by the average frequency of heterozygotes per locus (H) and by the proportion of polymorphic loci in the population (P). The first statistic (H) is the expected frequency of heterozygotes that would exist under a Hardy-Weinberg equilibrium, and is an average of all the loci sampled (Nei, 1975). The proportion of polymorphic loci (P) is calculated using two criteria: (a) a locus is considered polymorphic if the frequency of the most common allele is not greater that 0.95; and (b) if the frequency is not greater than 0.99. Average heterozygosities and the proportion of polymorphic loci are given in Table 3. The overall mean heterozygosity for all the populations sampled is 0.0885, which is within the range reported for other rodents (Ayala, 1975). The San Carlos population has the highest H (0.1533) and La Trilla the lowest (0.0589). The overall mean proportion of polymorphic loci for all population is 18.2% and 20.5% depending respectively on whether the .95 or .99 criterion is used. Again San Carlos has the greatest proportion of polymorphic loci (36.4% and 45.5% respectively) while La Trilla has the least (9,1% and 9.1%).

To measure genetic divergence between populations, we used Nei's (1975) indices of 'genetic identity' (I) and 'genetic distance' (D). Both statistics were calculated for all possible pairwise comparisons between populations and are given in Table 4. The overall mean genetic identity for all 15 comparisons is $\bar{I} = 0.942 \pm 0.011$. Mean identity within the *P. guairae*

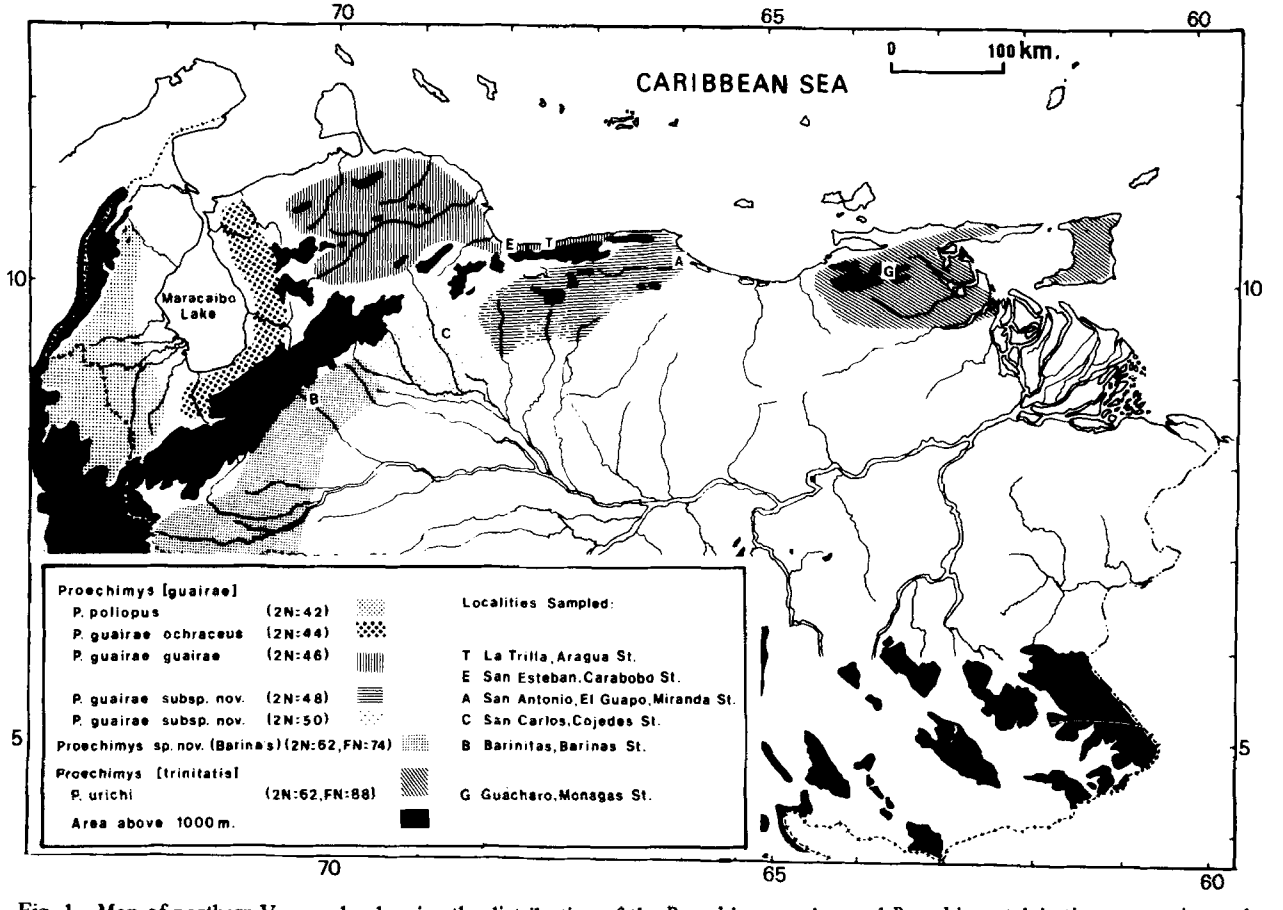

Fig. 1. Map of northern Venezuela, showing the distribution of the *Proechimys guairae* and *Proechimys trinitatis* superspecies, and the location of the sampled localities. Superspecies are indicated by square brackets.

Table 2

Allelic frequencies for variable loci in six populations of *Proechimys*. Sample sizes are given in parentheses

Locus and Allele	Populations *Proechimys guairae* complex La Trilla	San Esteban	San Antonio	San Carlos	Barinitas	*P. urichi* Guácharo
Adkin	(19)	(12)	(23)	(14)	(16)	(22)
a	0.0000	0.0000	0.0000	0.0357	0.0000	0.0000
b	1.0000	1.0000	1.0000	0.9643	1.0000	1.0000
αGpdh	(19)	(12)	(22)	(14)	(16)	(20)
a	0.0000	0.0000	0.0455	0.0000	0.0000	0.0000
b	1.0000	1.0000	0.9545	1.0000	1.0000	1.0000
Gal	(19)	(12)	(23)	(14)	(16)	(16)
a	0.0000	0.0000	0.0000	0.1429	0.0000	0.0000
b	1.0000	1.0000	1.0000	0.8571	1.0000	1.0000
G-6pgdh	(19)	(9)	(23)	(13)	(16)	(22)
a	1.0000	1.0000	1.0000	0.8462	1.0000	1.0000
b	0.0000	0.0000	0.0000	0.1538	0.0000	0.0000
Got-1	(19)	(12)	(23)	(14)	(16)	(22)
a	0.0000	0.0000	0.0000	0.0357	0.0000	0.0000
b	1.0000	1.0000	1.0000	0.9643	1.0000	1.0000
Hb	(19)	(12)	(19)	(13)	(16)	(22)
a	0.0000	0.0000	0.3158	0.6154	0.5625	0.7727
b	1.0000	1.0000	0.6842	0.3846	0.4375	0.2273
Lap	(16)	(11)	(13)	(11)	(11)	(13)
a	0.0000	0.0000	0.0000	0.0000	0.0000	0.1538
b	0.0000	0.0000	0.3462	0.0000	0.0000	0.0385
c	0.0000	0.0000	0.0000	0.0000	0.0000	0.1538
d	0.1563	0.0000	0.0382	0.0000	0.0909	0.0000
e	0.0938	0.0000	0.0385	0.0000	0.2273	0.1154
f	0.2500	0.3182	0.0385	0.0000	0.0909	0.0385
g	0.2811	0.2727	0.0000	0.4545	0.1818	0.3462
h	0.0000	0.0455	0.1154	0.0455	0.0455	0.0000
i	0.0625	0.1818	0.3462	0.3636	0.3181	0.0000
j	0.1563	0.1818	0.0385	0.0909	0.0455	0.0769
k	0.0000	0.0000	0.0000	0.0455	0.0000	0.0769
l	0.0000	0.0000	0.0385	0.0000	0.0000	0.0000
Mpi	(16)	(7)	(23)	(14)	(16)	(21)
a	0.0000	0.0000	0.0000	0.0000	0.0313	0.0000
b	1.0000	0.5114	1.0000	0.6071	0.9374	1.0000
c	0.0000	0.0000	0.0000	0.0714	0.0000	0.0000
d	0.0000	0.4286	0.0000	0.0000	0.0000	0.0000
e	0.0000	0.0000	0.0000	0.2857	0.0313	0.0000
f	0.0000	0.0000	0.0000	0.0358	0.0000	0.0000
6-pgdh	(18)	(10)	(23)	(13)	(16)	(20)
a	0.0000	0.0000	0.0000	0.0769	0.0000	0.1000
b	1.0000	0.7000	1.0000	0.8462	1.0000	0.0500
c	0.0000	0.1000	0.0000	0.0769	0.0000	0.8500
d	0.0000	0.2000	0.0000	0.0000	0.0000	0.0000
To	(19)	(11)	(23)	(14)	(16)	(22)
a	0.0000	0.0000	0.0000	0.2143	0.0000	1.0000
b	1.0000	1.0000	1.0000	0.7857	1.0000	0.0000

Table 2 (contd)

Allelic frequencies for variable loci in six populations of *Proechimys*. Sample sizes are given in parentheses

Locus and Allele	Populations *Proechimys guairae* complex La Trilla	San Esteban	San Antonio	San Carlos	Barinitas	*P. urichi* Guácharo
Xdh	(17)	(9)	(21)	(10)	(15)	(20)
a	0.0000	0.0000	0.0000	0.0769	0.0000	0.1000
b	1.0000	0.7000	1.0000	0.8462	1.0000	0.0500
c	0.0000	0.1000	0.0000	0.0769	0.0000	0.8500
d	0.0000	0.2000	0.0000	0.0000	0.0000	0.0000

Table 3

Average heterozygosity per locus (H) and proportion of polymorphic loci (P) for populations of *Proechimys guairae* and *P. urichi*. P' and P" refer to the '0.95' and '0.99' polymorphism criteria, respectively.

Population	H ± s.e.	P'	P"
P. guairae			
La Trilla	0.0589 ± 0.0418	9.1	9.1
San Esteban	0.1045 ± 0.0496	13.6	13.6
San Antonio	0.0650 ± 0.0383	13.6	18.2
San Carlos	0.1533 ± 0.0462	36.4	45.5
Barinitas	0.0695 ± 0.0495	18.2	18.2
mean	0.0902 ± 0.0176	18.2 ± 4.8	20.9 ± 5.8
P. urichi			
Guácharo	0.0798 ± 0.0420	18.2	18.2
Mean	0.0885 ± 0.0145	18.2 ± 3.9	20.5 ± 5.22

Table 4

Genetic distance (upper triangle) and genetic identity (lower triangle) for populations of *P. guairae* and *P. urichi*

	La Trilla (T)	San Esteban (E)	*P. guairae* complex San Antonio (A)	San Carlos (C)	Barinitas (B)	*P. urichi* Guácharo (G)
T	–	0.014	0.023	0.036	0.029	0.134
E	0.986	–	0.035	0.039	0.043	0.134
A	0.976	0.966	–	0.033	0.046	0.146
C	0.965	0.962	0.968	–	0.025	0.087
B	0.972	0.958	0.956	0.976	–	0.103
G	0.877	0.877	0.868	0.918	0.905	–

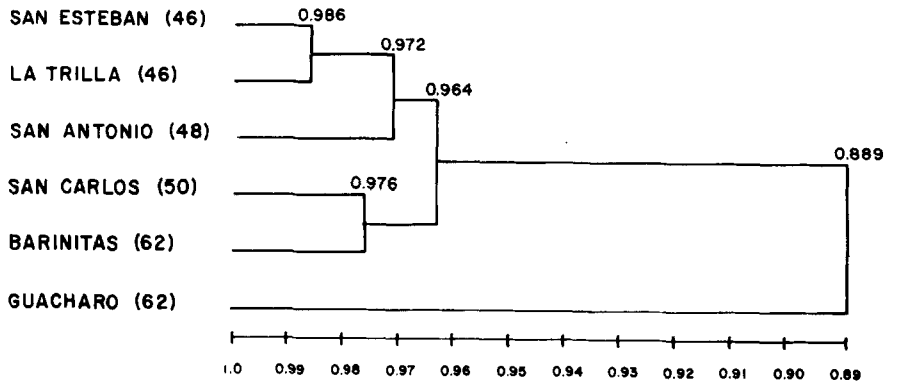

Fig. 2. Dendrogram based on Nei's I. Clustering is by unweighted pair group method. Chromosome numbers are given in parenthesis for each population.

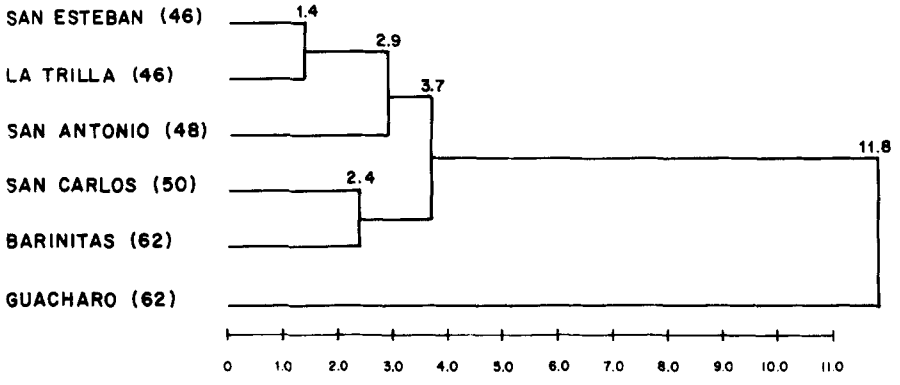

Fig. 3. Dendrogram based on Nei's D x 10^{-2}. Clustering is by unweighted pair group method. Chromosome numbers are given in parenthesis for each population.

complex is 0.969 ± 0.003 for all 10 pairwise comparisons; mean identity between *P. urichi* and the *P. guairae* complex is 0.889 ± 0.011 for all five comparisons. Thus, it is apparent that the karyomorphs of the *P. guairae* complex are more closely related among themselves than this complex to *P. urichi*. Within the *P. guairae* complex, increased genetic divergence and higher chromosome number are roughly correlated. Thus, for the two 2n = 46 populations, I = 0.986; between the 2n = 46 and 2n = 48 karyomorphs I = 0.971; and I = 0.968 between 2n = 48 and 2n = 50, and so on. We used the unweighted pair group method to generate dendograms based on genetic identities (Fig. 2) and genetic distances (Fig. 3). It is evident that genetic divergence and chromosome number are correlated within *P. guairae* and that the complex of *P. guairae* karyomorphs are a group distinct from *P. urichi*.

Discussion

Within the chromosomal Rassenkreis of *P. guairae*, there is a transition from 2n = 42 to 2n = 44, which involves one Robertsonian change and three pericentric inversions; a single Robertsonian change accounts for the difference between the 2n = 44 to 2n = 46 chromosomal races. Similarly, one change of the fission type accounts in each case for the difference between the 2n = 46 and 2n = 48 between the 2n = 48 and 2n = 50 karyotypes. The karyotype of the 2n = 62 population can be derived from the 2n = 50 one by six Robertsonian fissions plus two pericentric inversions. Differences between *P. guairae* and *P. urichi* (2n = 62, FN = 88) have not been worked out. It is reasonable to assume that reproductive isolation occurs between 2n = 50 and 2n = 62 populations of *P. guairae* (Reig et al., 1978, 1979). Isolation between

the 2n = 46, 2n = 48, and 2n = 50 karyomorphs is less certain; however the following facts suggest that they are genetically isolated semispecies: (i) each form has a definite parapatric area of distribution (Fig. 1); (ii) chromosomal polymorphism within and between morphs is almost inexistent; (iii) there are no clines within any chromosomal type. In other words, there is an abrupt transition from one form to the other. This indicates that although one or two Robertsonian changes may not prevent gene flow between karyomorphs (White, 1973), in our case they are doing so. This pattern of chromosome differentiation in *P. guairae* is similar to what Patton & Gardner (1972) reported in populations of *Proechimys* in Perú. Assuming that *P. guairae* populations are at least semispecies, we ask, then, how much genetic differentiation there exists among them? As a paradigm of speciation, *Drosophila willistoni* is a nice example to start with. Genetic identity is 0.798 among semispecies of *D. willistoni* (Ayala, 1975). It is clear that *P. guairae* karyomorphs are genetically very similar under this paradigm of speciation: in fact, $\bar{I}$ = 0.970 for local populations of *D. willistoni* and $\bar{I}$ = 0.969 for semispecies of *P. guairae*. Moreover, genetic identity between the sibling species *P. guairae* and *P. urichi* is 0.880. For sibling species of *D. willistoni*, genetic identity is 0.563, 37% smaller. Spiny rats do not follow a pattern of speciation through increasing genetic divergence as *D. willistoni*; comparison with other rodents is in order.

Available data on genetic differentiation and speciation in rodents can be treated separately for fossorial and non-fossorial ones. Fossorial rodents seem to follow two broad patterns of speciation (Patton & Yang, 1977): (i) species complexes with extensive chromosome differences associated with reproductive isolation and low genetic variability, and (ii) species with extensive allozymic and chromosomal differentiation and no reproductive barriers associated with karyotypic variation. Pattern (i) is well exemplified by the mole rat, *Spalax ehrenbergi* (Nevo & Shaw, 1972), and by the pocket gophers of the *Thomomys talpoides* complex (Nevo et al, 1974) and *Geomys bursarius* group (Selander et al, 1974). Average heterozygosities for these rodents are 0.037, 0.047, and 0.040, respectively. The overall mean heterozygosity for rodents is 0.057 (Dobzhansky et al, 1977; Selander, 1976). Hence, Venezuelan *Proechimys* are genetically more variable than these fossorial forms, and are more heterozygous than the 'average' rodent as well. The average identity among karyomorphs of *S. ehrenbergi* is 0.978 and for *T. talpoides* $\bar{I}$ = 0.925, so mole rats and pocket gophers show little genetic divergence. The species of the *Geomys bursarius* group are equally very closely related, 72% to 83% of predominant alleles are shared by all species pairs of the group. Thus, chromosomal forms of *Proechimys* have similar levels of genetic identity as occurs in *Spalax*, *Thomomys* and *Geomys*.

Extensive genetic and chromosome variation without any concomitant development of reproductive isolation has been reported for *Thomomys bottae* (Patton & Yang, 1977), which fits pattern ii) above. For *T. bottae*, the mean heterozygosity is 0.093, approximately the same as *Proechimys*. Populations of *T. bottae* are not reproductively isolated and have a mean genetic identity of 0.87, much lower than populations of Venezuelan spiny rats.

The cotton rats *Sigmodon hispidus* and *S. arizonae* are non-fossorial sibling species that inhabit an extensive area in the United States and Mexico (Johnson et al., 1972). The mean allozymic heterozygosity is rather low (2%-3%), lower than in Venezuelan spiny rats. Conspecific populations show little genetic divergence, Roger's S coefficient is 0.983. Thus conspecific populations of cotton rats show similar levels of genetic identity as karyomorphs of the *P. guairae* complex (cf. Chakraborty & Tateno, 1976).

Kangaroo rats (*Dipodomys*) are non-fossorial rodents of the western United States and northern Mexico. They have less heterozygosity (H = 0.02) than Venezuelan spiny rats and they show moderate interspecific divergence (S = 0.61). Roger's coefficient for conspecific population always exceeds 0.90 (Johnson & Selander, 1971).

The data reviewed in the previous paragraphs are summarized on a qualitative basis in Table 5. All rodents in this table, with the exception of *T. bottae* have in common a high interpopulational genetic similarity and isolation as a consequence of chromosome divergence, irrespective of whether they are fossorial or not. On the other hand, both the fossorial and temperate gopher (*T. bottae*) and the tropical non fossorial spiny rat (*Proechimys*) have high genetic heterozygosity. Therefore, it seems that any hypothesis to explain patterns of speciation in rodents can be either an 'ad hoc' hypothesis for a particular species, or a very general one that has little predictive power.

Table 5

Quantitative assessment of speciation patterns in rodents

Organism	Fossorial?	High Heterozygosity?	High Genetic similarity?	Chromosomally isolated?	Sibling Species	Tropical?	Reference
Spalax ehrenbergi	√		√	√	√		Nevo & Shaw, 1972.
Thomomys talpoides	√		√	√	√		Nevo et al, 1974.
Thomomys bottae	√	√					Patton & Yang, 1977.
Geomys	√		√	√			Selander et al, 1974.
Sigmodon			√	√	√		Johnson et al, 1972.
Dipodomys			√	√	√		Johnson & Selander 1971.
Proechimys		√	√	√	√	√	This paper

To illustrate this, we offer some estimates of divergence times between karyomorphs of Venezuelan spiny rats (see also Nevo et al., 1974 and Patton & Yang, 1977). Nei's equation (Nei, 1975) estimates approximately 50,000 years for the divergence of karyomorphs within the *P. guairae* complex and 200,000 years for the separation of *P. guairae* from *P. urichi*. These ages coincide with Pleistocene glacial periods and the formation of ecological islands of 'refugia' throughout temperate and tropical America. Indeed, such changes could be very important to speciation events. In fact, they have been set forth to explain speciation in organisms as different as butterflies (Turner, 1976), birds (Haffer, 1969), and rodents (Patton & Yang, 1977). Similar explanations could be made for *Proechimys*, but we think it would contribute little toward explaining why speciation occurs both in fossorial and non fossorial rodents through chromosomal changes with little protein divergence. Moreover, we can offer no explanation for the correlation between chromosome number and genetic distance found in Venezuelan spiny rats.

Recently, Wilson and his collaborators (Wilson, Sarich & Maxson, 1974) have suggested that morphology, chromosome systems, and proteins evolve at different rates in mammals. They conclude that rapid chromosome rearrangements in mammals parallels their rapid morphological evolution but that proteins evolve at a much slower rate. Our data for Venezuelan spiny rats provide a counterexample to this hypothesis, since karyomorphs of *Proechimys* are morphologically very little differentiated.

The authors are indebted to Miss Lorraine Barr and to Mrs. María Alicia Barros for expert technical assistance. They are also indebted to Dr. Michael Robinson for his advice and to Miss Gisela García who helped with some of the calculations. Robert Tonn, Julio González, Witremundo Torrealba, Alejandro Reig and Carmen V. Alvarez are also acknowledged for providing some specimens and help during our field work.

This work was supported by a grant from the 'Consejo Nacional de Investigaciones Científicas y Tecnológicas de Venezuela', (CONICIT, S1-0630).

References

Aguilera, M., O.A. Reig, M.A. Barros & M.G. Basáñez (1979). Sistemática, citogenética y datos reproductivos de una población de P. canicollis del noroeste de Venezuela. *Acta cient. venez.* (in press).

Ayala, F.J. (1975). Genetic differentiation during the speciation process. *Evol. Biol.* 8: 1-78.

Ayala, F.J., J.R. Powell, M.L. Tracey, C.A. Mourao & S. Pérez-Salas (1972). Enzyme variability in the Drosophila willistoni group. IV. Genic variation in natural populations of Drosophila willistoni. *Genetics.* 70: 113-139.

Chakraborty, R. & Y. Tateno (1976). Correlations between some measures of genetic distance. *Evolution* 30: 851-853.

Dobzhansky, T., F.L. Ayala, G.L. Stebbins & J.W. Valentine (1977). Evolution W.M. Freeman, San Francisco.

Haffer, J. (1969). Speciation in Amazonian forest birds. *Science*, 165. 131-137.

Handley, C.O. (1976). Mammals of the Smithsonian Venezuelan project. *Brigham Young Univ. Stud.* Vol XX, 5: 1-91.

Johnson, W.E. & R.K. Selander (1971). Protein variation and systematics in kangaroo rats (genus Dipodomys). *Syst. Zool.* 20: 377-405.

Johnson, W.E., R.K. Selander, M.H. Smith & Y.J. Kim (1972). Biochemical genetics of sibling species of cotton rat (Sigmodon). Studies in genetics VII. *Univ. Tex. Publs.* 7213: 297-305.

Nei, M. (1975). Molecular population genetics and evolution. North Holland, Amsterdam.

Nevo, E. & C.R. Shaw, (1972). Genetic variation in a subterranean mammal, Spalax ehrenbergi. *Biochem. Genetics* 7: 235-241.

Nevo, E., Y.J. Kim, C.R. Shaw & C.S. Thaeler, Jr. (1974). Genetic variation, selection and speciation in Thomomys talpoides pocket gophers. *Evolution.* 28: 1-23.

Patton, J.L. & A.L. Gardner (1972). Notes on the systematics of Proechimys (Rodentia: Echimyidae), with emphasis on peruvian forms. Occas. *Pap. Mus. Zool., La. State Univ.* 44: 1-30.

Patton, J.L. & S.Y. Yang (1977). Genetic variation in Thomomys bottae pocket gophers: macrogeographic patterns. *Evolution* 31. 697-719.

Reig, O.A., M. Aguilera, M.A. Barros & M. Useche (1978). A Rassenkreis of chromosome forms in Venezuelan spiny rats of the Proechimys guairae superspecies (Rodentia: Echimyidae). Absts. Pap. II Congr. Theriol. Internat. 20-27 June, 1978. Brno. Czechoslovakia: 74.

Reig, O.A., M. Aguilera, M.A. Barros & M. Useche (1979). Chromosome speciation in a Rassenkreis of Venezuelan spiny rats (Genus Proechimys, Rodentia, Echimyidae). In: N.N. Vorontzov ed. Animal Genetics and Evolution. Junk The Hague (in press).

Reig, O.A., M.A. Barros, M. Useche, M. Aguilera & O.J. Linares (1979b). The chromosomes of spiny rats, Proechimys trinitatis, from Trinidad and eastern Venezuela (Rodentia, Echimyidae). Genetica, in press.

Reig, O.A., P. Kiblisky & I. Löbig. (1970). Isomorphic sex-chromosomes in two Venezuelan populations of the spiny rats, genus Proechimys (Rodentia, Caviomorpha) *Experientia* 26: 201-202.

Reig, O.A., M. Tranier & M.A. Barros. (1979). Sur les chromosomes des Proechimys de la Guyane Française, de la Guyane Vénézuélienne et de Belem (Brazil) (Rodentia, Echimyidae) *Mammalia* (in press).

Reig, O.A. & M. Useche. 1976. Diversidad cariotípica y sistemática en problaciones venezolanas de Proechimys (Rodentia, Echimyidae), con datos adicionales sobre poblaciones de Perú y Colombia. *Acta cient. venez.* 27: 132-140.

Selander, R.K. (1976). Genic variation in natural populations. In: F.J. Ayala, ed. Molecular Evolution. Sinauer, Massachusetts, 1976.

Selander, R.K., M.H. Smith, S.Y. Yang, W.E. Johnson & J.B. Gentry (1971). Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the old-field mouse (Peromyscus polionotus). Studies in Genetics VI, *Univ. Tex. Publs.* 7103. 49-90.

Selander, R.K., D.W. Kaufman, R.J. Baker & S.L. Williams (1974). Genic and chromosomal differentiation in pocket gophers of the Geomys bursarius group. *Evolution* 28: 557-564.

Turner, J.R.G. (1976). Adaptive radiation and convergence in subdivisions of the butterfly genus Heliconius (Lepidoptera: Nymphalidae). *Zool. J. Linn. Soc.* 58: 297-308.

White, M.J.D. (1973). Chromosomal rearrangements in mammalian population, polymorphism and speciation. In: A.B. Chiarelli & E. Capanna eds, Cytotaxonomy and Vertebrate evolution: 95-128. Academic Press., London.

Wilson, A.C., V.M. Sarich & L.R. Maxson (1974). The importance of gene rearrangement in evolution: evidence from studies on rates of chromosomal, protein and anatomical evolution. *Proc. natn. Acad. Sci. USA* 71: 3028-3030.