Extreme Chromosomal Polytypy in a Population of *Sceloporus grammicus* (Sauria: Phrynosomatidae) at Santuario Mapethé, Hidalgo, México

IRENE GOYENECHEA, FERNANDO MENDOZA-QUIJANO,
OSCAR FLORES-VILLELA, AND KENT M. REED[1]

*Museo de Zoologia, Facultad de Ciencias, Universidad Nacional Autonoma de México, A.P. 70-399,
México D.F., 04510, Mexico and*
[1]*Department of Biological Sciences, University of Wisconsin–Milwaukee, Milwaukee, Wisconsin 53201, USA*

ABSTRACT.—The karyotypic status of the mesquite lizard, *Sceloporus grammicus,* was investigated at two localities at Santuario Mapethé, Hidalgo, México. A total of 23 different karyotypes was recorded from the 36 individuals examined. Individual lizards were heterozygous at up to four chromosomes. Karyotypic differences were attributed to Robertsonian fission/fusions and pericentric inversions involving the macrochromosomes. The polymorphisms generally conformed to Hardy-Weinberg equilibrium suggesting a lack of underdominance for most rearrangements. The extreme chromosomal polytypy observed at Santuario Mapethé is hypothesized to result from parapatric hybridization between two chromosome races.

RESUMEN.—Se estudió el estatus cariotípico de la lagartija *Sceloporus grammicus* de dos localidades en Santuario Mapethé, Hidalgo, México. Se registraron un total de 23 cariotipos diferentes de 36 individuos examinados. Las largartijas fueron heterocigotas hasta en 4 pares cromosómicos. Las diferencias cariotípicas se atribuyeron a fisiones/fusiones Robertsonianas y a inversiones pericéntricas ue involucran a los seis pares macrocromosómicos. Los polimorfismos se conformaron generalmente de acuerdo al equilibrio Hardy-Weinberg, lo que sugiere uan ausencia de subdominancia para la mayoría de los rearreglos. La extrema politipia cromosómica observada parece ser el resultado de hibridación parapátrica entre dos razas cromosómicas.

Few species of vertebrates exhibit the extreme chromosomal polytypy observed in the mesquite lizard *Sceloporus grammicus* complex. Previous cytogenetic studies revealed eight distinct chromosome races in a relatively small area of the central Mexican plateau (Hall, 1983; Porter and Sites, 1986; Arévalo et al., 1991; Sites, 1993). The races (cytotypes) are defined primarily by Robertsonian (centric fission) rearrangements and include LS (Low Standard, 2n = 32♀), HS (High Standard, 2n = 32), F6 (2n = 34), F5 (2n = 34), F5+6 (2n = 36), FM1 (2n = 40–44), FM2 (2n = 44–46), and FM3 (2n = 38–42). In addition to the fixed differences which
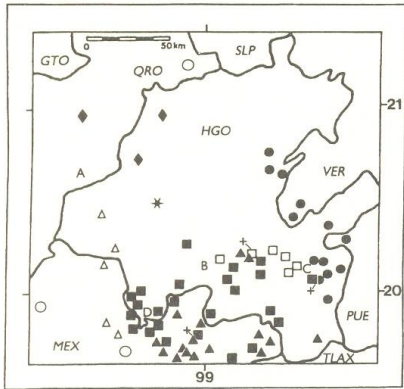
FIG. 1. Distribution of central Mexico cytotypes of *Sceloporus grammicus* (modified from Arévalo et al., 1991). Symbols for cytotypes: closed triangles = LS and HS; closed circles = F5; closed squares = FM2; closed diamonds = F5+6; open circles = F6; open triangles = FM1; open squares = FM3; star = Santuario Mapethé. Crosses indicate three documented hybrid zones and A–D denote four highly polymorphic populations of possible hybrid origin (A, Vizarrón; B, Fray Francisco; C, Huasca; D, Tepeji del Rio).

define the cytotypes, within-population pericentric inversion and/or Robertsonian polymorphisms are also present in several cytotypes (Sites, 1983; Porter and Sites, 1985, 1987; Reed et al., 1992b, c). Molecular phylogenetic studies have established the 2n = 32 karyotype (all macrochromosomes metacentric) as ancestral with the derivation of the races generally proceeding by increasing diploid number, although clearly refusion of previously fissioned chromosomes has occurred (Sites and Davis, 1989; Arévalo et al., 1994).

Sceloporus grammicus populations of central México have been extensively surveyed over the past two decades. Hall (1973, 1983; Hall and Selander, 1973) and Sites and co-workers (Sites, 1983; Porter and Sites, 1985; Arévalo et al., 1991) have revealed at least eight separate hybrid zones between six different combinations of cytotypes. The known hybrid zones include, HS × FM3 (Hidalgo), HS × F6 (México and Distrito Federal), LS × F6 (Morelos), LS × FM2 (México, 2 localities), F5 × FM2 (Hidalgo), and F5+6 × FM1 (Querétaro). Additional contacts are suspected based on chromosomal and molecular data.

Mesquite lizards from the Mexican state of Hidalgo have been well studied because of the occurrence within the state of five cytotypes including all three multiple fission (FM) races.

However, there are still large areas of potential *S. grammicus* habitat that have not been surveyed. The region of central Hidalgo is of particular interest because of the proximity of several divergent cytotypes (Fig. 1). In this paper, we report on a karyotypic survey of lizards from the vicinity of Santuario Mapethé, Hidalgo and present data consistent with a new chromosomal hybrid zone for the *Sceloporus grammicus* complex.

MATERIALS AND METHODS

Study Area.—Santuario Mapethé is located in the municipality of Cardonal, Hidalgo, 29 km NW Ixmiquilpan City (99°08'07"W and 20°39'06"N) at an elevation between 2400 and 2700 m. Vegetation surrounding the site is predominantly xeric shrub (*Hechtia, Dasylirion, Yucca,* and *Opuntia*) and *Quercus* forest is found at elevations above 2600 m. Daily temperatures vary from 12 to 26 C with an average annual rainfall of 270 mm (Rzedowski, 1981). Lizards were sampled from two areas during six collecting trips made during the period from January to October 1992. Locality I included two sites separated by a road and located 0.30 and 0.35 km SE of Santuario Mapethé (approximate straight line distance from the town church) at an elevation of 2410 m. Lizards captured at these two sites were pooled for subsequent analyses because the distance between them (approximately 50 m) is easily within the dispersal ability of an individual lizard (Sites et al., 1995). Lizards collected at this locality were found on *Agave* and *Opuntia* bordering cultivated fields. The second locality was located along a transect between *Agave* and *Quercus* forest, 1.5 km W Santuario Mapethé at 2400–2690 m.

Methods.—All lizards were captured either by hand, noose, or by stunning with rubber bands. Lizards captured alive were processed for mitotic karyotypes as described by Porter and Sites (1985) and Reed et al. (1992a). Chromosome preparations were silver-stained (Howell and Black, 1980) to score the morphology of chromosome 2 which carries the nucleolar-organizing regions (NORs) in this species. Specimens were deposited in the herpetological collection of the Museo de Zoologia "Alfonso L. Herrera" Facultad de Ciencias UNAM (MZFC).

The karyotype of each animal was scored from a minimum of five cells. Chromosomes were ordered by size following Hall (1973), Sites (1983), and Reed et al. (1992a). We used the abbreviations of Arévalo et al. (1991) to describe the morphology ("genotype") of the macrochromosomal complement. We designated the ancestral biarmed (nonfission) chromosome morphology as "A" and fission rearrangements as "B." Two types of inversions have occurred
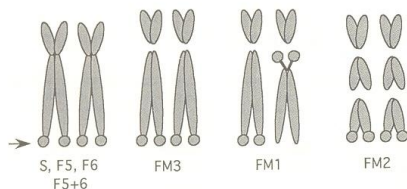
FIG. 2. Idiogram depicting the chromosome 2 morphologies observed in the *Sceloporus grammicus* complex (after Reed et al., 1992c). Circles denote the nucleolar organizer regions (NORs; arrowhead).

in the species complex. Inversions of the ancestral biarmed chromosomes were coded as "C," whereas inversions of fission products were denoted "D." Chromosomes 1, 2, and 6 can be unambiguously identified but chromosomes 3 and 4 are morphologically indistinguishable. Therefore heteromorphisms occurring at chromosomes 3 and 4 were assigned to chromosome 4 for consistency with previous cytotype designations. Coded genotypes were analyzed using Biosys-1 (Swofford and Selander, 1989). Chi-square tests for deviation from Hardy-Weinberg equilibrium were performed on the chromosomal frequencies using Levene's correction for small sample size.

Besides diploid number and general chromosomal morphology, the position of nucleolar organizer regions (NORs) provides an easily identifiable marker for distinguishing several of the cytotypes (Reed et al., 1992c). The karyotype of *S. grammicus* has a single pair of NORs (Fig. 2). In the Standard (LS and HS), F5, F6, and F5+6 cytotypes the NORs are positioned distally on the second largest macrochromosome. In each of the FM cytotypes, chromosome 2 has undergone rearrangements and is no longer present as a single metacentric element. In the FM3 cytotype, chromosome 2 has undergone centric fission and is represented by two acrocentric elements, one representing the long arm of the ancestral submetacentric chromosome and the second representing the short arm. The NORs in this cytotype retain their distal position on the larger element (Fig. 2). The FM1 cytotype shares the fission rearrangement found in the FM3 cytotype but, in addition, is polymorphic for an inversion of the large (NOR-bearing) acrocentric element. A unique chromosome morphology is found in the FM2 cytotype where chromosome 2 is represented by three acrocentric elements.

RESULTS

The karyotypes of *S. grammicus* individuals in the vicinity of Santuario Mapethé show ex-

treme complexity. We recorded a total of 23 different karyotypes among the 36 individuals examined from our two collecting localities (Table 1). Diploid numbers ranged from 34 to 44. With one exception (see below), all lizards were homozygous for the acrocentric (B) morphology of chromosome 5. Therefore, the variation in diploid number was due to the morphological condition of the remaining macrochromosomes (1, 2, 3, 4, and 6).

Locality I.—A total of 18 different karyotypes from 28 lizards was observed at locality I (Table 1). Individuals in this population were heterozygous at up to four chromosomes (Fig. 3). The most common karyotype at this locality was characterized as homozygous for fission of chromosomes 1, 3, 5, and 6 and heterozygous at chromosomes 2 and 4. This configuration was present in five lizards (MZFC 5978-69, 5978-70, 5978-74, 5978-75 and 5978-77; Table 1). Within individual lizards, chromosomes 3 and 4 ranged from all metacentric (AAAA) to all acrocentric (BBBB; Table 1). One lizard (MZFC 5978-73) was unique in that its karyotype included a small submetacentric chromosome (Fig. 3). Presence of this element is interpreted as a fusion of two different sized elements corresponding in size to chromosomes 5 and 6.

The fission morphologies of chromosomes 1 and 6 were the most common at locality I and were present at frequencies of 0.929 and 0.852, respectively (Table 2). Silver-staining of the NORs revealed the presence of three morphologies of chromosome 2. The frequencies of the three chromosomal types were approximately equal (A = 0.304, B = 0.393, and D = 0.304). The observed frequencies of chromosomes 3 and 6 did not significantly differ from those expected under Hardy-Weinberg equilibrium ($X^2 = 7.057$, df = 3, $P = 0.70$, and $X^2 = 0.703$, df = 1, $P = 0.402$, respectively). However, the observed frequencies of chromosome 1 were significantly different ($X^2 = 8.148$, df = 1, $P = 0.004$), showing a deficiency of heterozygotes. This deviation remained even when the data were analyzed at the subpopulation level (0.3 and 0.35 km SE Santuario Mapethé) indicating that the deficiency of heterozygotes was not due to Wahlund effect.

Locality II.—Five different karyotypes (Table 1) were recorded from the eight lizards collected at locality II. Similar to locality I, individuals in this population were heterozygous at up to four chromosomes. However, the most frequent karyotype (4 of 8 individuals) included chromosomes 1, 2, 3, and 6 as metacentrics, and chromosome 4 was polymorphic for inversion. Individuals with this karyotype were taken from oak forest. Whereas five lizards were heterozygous for the inversion of chromosome 4,

TABLE 1. Macrochromosomal genotypes of the lizards examined in this study. With the exception of MZFC 5978-73 (5+6 fusion heterozygote) all lizards were homozygous for the fission morphology (BB) at chromosome 5.

MZFC#	Sex	2n	Chrm1	Chrm2	Chrm3+4	Chrm6
Locality I						
5978-67	♀	42	BB	BB	ABBB	AB
5978-68	♀	42	BB	BB	AABB	BB
5978-69	♀	42	BB	AB	ABBB	BB
5978-70	♀	42	BB	AB	ABBB	BB
5978-71	♀	40	BB	AA	AABB	BB
5978-73	♀	38	BB	BB	AAAB	B*
5978-74	♀	42	BB	AB	ABBB	BB
5978-75	♀	42	BB	AB	ABBB	BB
5978-77	♀	42	BB	AB	ABBB	BB
5978-78	♀	40	BB	AA	AABB	BB
5978-80	♀	38	AB	AD	AAAA	AB
5978-81	♂	40	BB	BB	AAAA	BB
5979-86	♂	42	BB	DD	ABBB	AB
5980-91	♀	43	AB	BD	BBBB	BB
5980-93	♀	41	BB	DD	AABB	AB
5980-95	♂	40	BB	AB	AAAB	AB
5980-96	♂	44	BB	DD	BBBB	BB
5980-97	♂	40	AA	BD	BBBB	BB
5981-102	♀	40	BB	DD	AAAA	BB
5981-103	♀	40	BB	AD	AAAB	BB
5981-104	♀	40	BB	AD	AAAB	BB
5981-105	♀	41	BB	DD	AABB	AB
5981-106	♀	41	BB	AB	ABBB	AB
5981-107	♂	41	BB	AB	ABBB	AB
5981-108	♀	40	BB	BB	AAAA	BB
5981-109	♀	41	BB	AD	AABB	BB
5981-110	♂	41	BB	AD	AABB	BB
5981-111	♂	42	BB	BB	AABB	BB
Locality II						
5999-142	♂	33	AA	AA	AAAC	AA
5999-143	♂	33	AA	AA	AAAC	AA
5999-144	♀	38	AB	AD	AAAB	AB
5999-145	♀	35	AA	AA	AAAC	AB
5999-146	♂	38	AB	AD	AABB	AB
5999-147	♂	33	AA	AA	AAAC	AA
5999-148	♂	39	BB	AD	ABBB	AA
5999-149	♂	33	AA	AA	AAAC	AA

no inversion homozygotes were obtained (Table 1).

The frequencies of the various chromosomal morphologies at locality II differed significantly from those at locality I (Table 2). Specifically, the karyotypes included a greater proportion of metacentric (A) chromosomes. At locality II the A morphology of chromosomes 1 and 6 was predominate (0.750 and 0.813, respectively). Two morphologies (A and D) of chromosome 2 were observed. As with chromosomes 1 and 6, the metacentric (A) morphology was most frequent (0.813). Although the sample size was small, the frequencies of all three unambiguous macrochromosomes (1, 2, and 6) did not differ significantly from Hardy-Weinberg expectations (chromosome 1, $X^2 = 1.432$, df = 1, $P = 0.231$, chromosome 2, $X^2 = 0.269$, df = 1, $P = 0.604$; chromosome 6, $X^2 = 0.269$, df = 1, $P = 0.604$).

DISCUSSION

The karyotypic status of *S. grammicus* at Santuario Mapethé is comparable to the highly polymorphic population near Cadereyta, Querétaro where eight different karyotypes were found in a sample of 24 lizards (Porter and Sites, 1985). Two contrasting hypotheses could account for the extreme chromosomal polytypy observed in our sample. One hypothesis is that the observed polymorphisms are "endemic" to this population, having arisen *in situ*. Several lizards in our sample carried the inversion morphology of chromosome 2 known only from the FM1 cytotype (Reed et al., 1992c). However, if
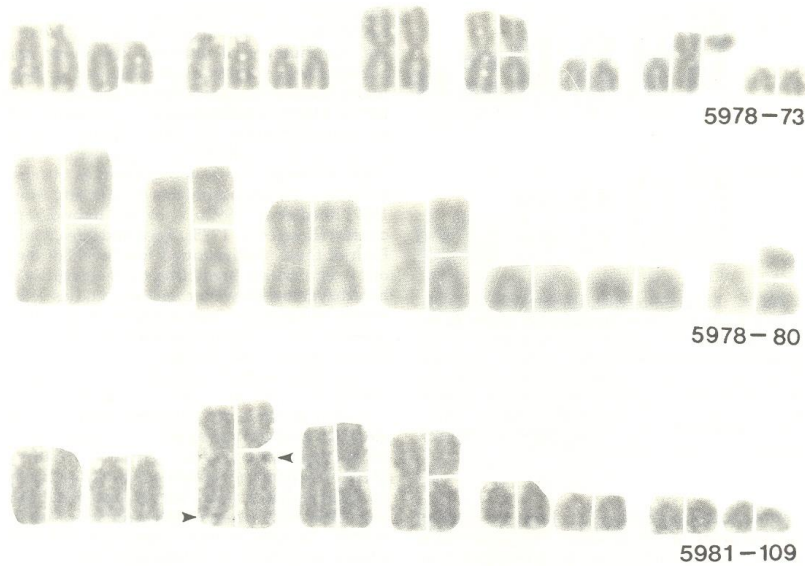
5978—73

5978—80

5981—109

Fig. 3. Partial somatic karyotypes representative of the macrochromosomal combinations of the individuals examined in this study. MZFC 5978-73 heterozygous for fission at chromosome 4 and fusion of chromosomes 5 and 6. MZFC 5978-80 heterozygous for fission of chromosomes 1, 2, 4, and 6. MZFC 5981-109 heterozygous for fission/inversion at chromosome 2 and heterozygous for fission at chromosomes 3 and 4. Arrowheads denote the position of the nucleolar organizer regions (NORs) in the chromosome 2 (AC) fission/inversion heterozygote MZFC 5981-109.

the ancestral population was FM1, a minimum of four additional chromosomal rearrangements (fusions of chromosomes 2, 3, and 6 and inversion of chromosome 4) are needed to account for all of the variation observed in our sample.

The alternative hypothesis is that this region represents a contact zone between two chromosome races. A hybrid zone involving the F5 and FM1 cytotypes is consistent with the chromosomal morphologies and polymorphisms observed at Santuario Mapethé (Fig. 4). Three

TABLE 2. Frequencies of chromosomal "alleles" at the two Santuario Mapethé localities and results of contingency chi-square analysis.

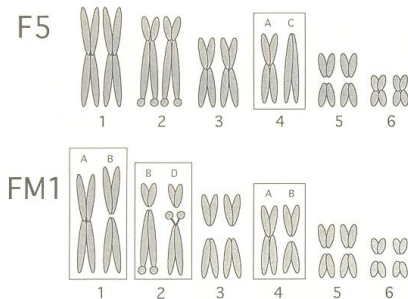|	Locality				
Locus	I	II	χ^2	df	P
CHRM-1			33.153	1	<0.00000
A	0.071	0.750			
B	0.929	0.250			
CHRM-2			14.625	2	0.00067
A	0.304	0.813			
B	0.393	0.000			
D	0.304	0.188			
CHRM-6			25.941	1	<0.00000
A	0.148	0.813			
B	0.852	0.188			
(Totals)			73.719	4	<0.00000

FIG. 4. Idiogram of macrochromosomal complements of the F5 (2n = 34) and FM1 (2n = 42–44) cytotypes of *Sceloporus grammicus*. Note the unambiguous fixed differences between the two at chromosomes 2 and 6, and the within-race heteromorphisms at chromosomes 1, 2, and 4 (enclosed in boxes). Circles mark locations of nucleolar organizer regions (NORs) on chromosome 2, and letters are genotype codes described in the text, and given in Table 1.

chromosomal morphologies argue in favor of involvement of the F5 race. The metacentric condition of chromosome 2 is known only from the non-FM cytotypes (S, F5, F6, F5+6). The fixed fission of chromosome 5 would eliminate two races (S and F6), and the metacentric condition at chromosome 6 eliminates all but the F5 race. As previously discussed, the inversion of chromosome 2 implicates the involvement of the FM1 race. We cannot, however, definitively rule out the involvement of other cytotypes. For example, the F5 and F5+6 cytotypes differ by a single rearrangement (fission of chromosome 6) and FM3 differs from FM1 by one fission/fusion rearrangement (chromosome 3) and the inversion of chromosome 2.

Several studies have shown an increased rate of chromosomal mutations in natural and/or experimental hybrids (Peters, 1982; Shaw et al., 1983; Hägele, 1984; Naviera and Fontdevila, 1985; Arévalo et al., 1991) and in *S. grammicus* (Porter and Sites, 1987). Hybrid populations may contain chromosomal morphologies not found in the parental taxa (see also Reed et al., 1995b). For example, the fusion of elements of two different chromosomes (chromosomes 5 and 6) seen at Locality I of the present study was observed in other hybrid populations of *S. grammicus* by Porter and Sites (1986, Cadereyta, Querétaro) and by Arévalo et al. (1991, Fray Francisco, Hidalgo). These authors concluded that these rearrangements had a mutational origin in these hybrid zones.

Based on our chromosomal data we can comment only briefly on the possible effects the

chromosomal polymorphisms observed at Santuario Mapethé may have on individual carriers. The number of different karyotypes and chromosomal combinations observed at Santuario Mapethé suggests that heterozygotes are fertile. Meiotic studies have demonstrated a lack of underdominance for simple fission and inversion polymorphisms in *S. grammicus* when these rearrangements were present as intrapopulational heteromorphisms (Porter and Sites, 1987; Reed et al., 1992b, c) or in a hybrid zone context (Reed et al., 1995a; Reed and Sites, 1995). Each of these studies found low levels of meiotic irregularities, predicting normal fertility of heterozygotes. However, meiotic studies often reveal complexities not apparent from direct observations of mitotic chromosomal polymorphisms (Reed et al., 1995b).

Additional support for a hybrid zone interpretation is the association of chromosomal variation at Santuario Mapethé with both an elevation gradient and an ecotone between xerophytic vegetation and oak forest. At Locality I (2410 m) where the habitat consisted primarily of *Agave* and rock walls, karyotypes were FM1-like. However, lizards with primarily "metacentric" karyotypes were taken from oak substrate at slightly higher elevations. Hybrid zone theory predicts that zones of hybridization will be centered in either troughs of low population density, or within ecotones between adjacent habitats (Barton and Hewitt, 1989; Harrison, 1991). In *S. grammicus*, several documented hybrid zones are associated with ecological transitions (Hall and Selander, 1973; Arévalo et al., 1993; Sites et al., 1993). Sites et al. (1995) demonstrated strong association between karyotype and habitat in the F5 × FM2 hybrid zone near Tulancingo, Hidalgo where F5 individuals predominated in oak forest and FM2 individuals elsewhere.

Distributional data provide little help in assessing the karyotypic status of the lizards at Santuario Mapethé. As shown in Fig. 1, there are huge distributional gaps in north-central Hidalgo. The nearest populations of the FM1 cytotype occur at Amealco, Hidalgo approximately 60 km to the southwest and populations of the F5 cytotype are known from localities approximately 75 km to the east (Fig. 1; Arévalo et al., 1991). Given the lack of karyotypic data from surrounding populations, this collection could easily document the eastern edge of FM1 and western edge of F5. Interestingly, populations of the F5+6 cytotype are found approximately 30 km to the northwest. The proximity of this cytotype to Santuario Mapethé argues for its involvement in hybridization at this locality as opposed to the F5 cytotype. Regardless of which cytotypes are involved, significant

range extensions are required if the localities examined in the present study do in fact represent a hybrid zone.

The karyotypic status of surrounding populations or the potential influences of human activity on lizard populations near Santuario Mapethé are unknown. Clearly analysis of molecular markers, population structure, and additional sampling of adjacent localities are needed to fully understand the origin of this highly polymorphic population. If our hybrid zone hypothesis is correct, the F5 × FM1 combination is most parsimonious in that it accounts for all of the observed chromosomal variation without postulating additional rearrangements. Confirmation of a F5 × FM1 hybrid zone would be noteworthy in that it would represent a contact between two closely related cytotypes differing by multiple rearrangements (Arévalo et al., 1994).

LITERATURE CITED

ARÉVALO, E., G. CASAS, S. K. DAVIS, G. LARA, AND J. W. SITES, JR. 1993. Parapatric hybridization between chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae): structure of the Ajusco transect. Copeia 1993:352–372.

———, S. K. DAVIS, AND J. W. SITES, JR. 1994. Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. Syst. Biol. 43:387–418.

———, C. PORTER, A. GONZALEZ, F. MENDOZA, J. L. CAMARILLO, AND J. W. SITES, JR. 1991. Population cytogenetics and evolution of the *Sceloporus grammicus* complex (Iguanidae) in Central Mexico. Herpetol. Monogr. 5:79–115.

BARTON, N. H., AND G. M. HEWITT. 1989. Adaptation, speciation, and hybrid zones. Nature 341:497–503.

HÄGELE, K. 1984. Different hybrid effects in reciprocal crosses between *Chironomus thummi thummi* and *C. t. piger* including spontaneous chromosome aberrations and sterility. Genetica 63:195–211.

HALL, W. P. 1973. Comparative population cytogenetics, speciation and evolution of the iguanid lizard genus *Sceloporus.* Ph.D. Diss., Harvard Univ., Cambridge.

———. 1983. Modes of speciation and evolution in the sceloporine iguanid lizards. I. Epistemology of the comparative approach and introduction to the problem. *In* A. G. J. Rhodin and K. Miyata (eds.) Advances in Herpetology and Evolutionary Biology, pp. 643–679. Mus. Comp. Zool., Cambridge, Massachusetts.

———, AND R. K. SELANDER. 1973. Hybridization of karyotypical differentiated population in the *Sceloporus grammicus* complex (Iguanidae). Evolution 27:226–242.

HARRISON, R. G. 1991. Hybrid zones: windows on evolutionary process, *In* D. Futuyma, and J. Antonovics (eds.), Oxford Surveys in Evolutionary Biology, Vol. 7, pp. 69–128. Oxford Univ. Press, London.

HOWELL, W. M., AND D. A. BLACK. 1980. Controlled silver-staining of nucleolus organizer regions with protective colloidal developer: a 1-step method. Experientia 36:1014–1015.

NAVIERA, H., AND A. FONTDEVILA. 1985. The evolutionary history of *Drosophila buzzati.* IX. High frequencies of new chromosome rearrangements induced by introgressive hybridization. Chromosoma 91:87–94.

PETERS, G. 1982. The recurrence of chromosome fusion interpopulation hybrids of the grasshopper *Atractomorpha similis.* Chromosoma 85:323–347.

PORTER, C. A., AND J. W. SITES, JR. 1985. Normal disjunction in Robertsonian heterozygotes from a highly polymorphic lizard population. Cytogenet. Cell Genet. 39:250–257.

———. 1986. Evolution of *Sceloporus grammicus* complex (Sauria: Iguanidae) in Central Mexico: population cytogenetics. Syst. Zool. 35:334–358.

———. 1987. Evolution of *Sceloporus grammicus* complex (Sauria: Iguanidae) in central Mexico. II. Studies on rates of nondisjunction and the occurrence of spontaneous chromosomal mutations. Genetica 75:131–144.

REED, K. M., AND J. W. SITES, JR. 1995. Female fecundity and mating preferences in a hybrid zone between chromosome races of the *Sceloporus grammicus* complex (Sauria, Phrynosomatidae). Evolution 49:61–69.

———, I. F. GREENBAUM, AND J. W. SITES, JR. 1995a. Cytogenetic analysis of chromosomal intermediates from a hybrid zone between two chromosome races of the *Sceloporus grammicus* complex (Sauria, Phrynosomatidae). Evolution 49:37–47.

———. 1995b. Dynamics of a novel chromosomal polymorphism within a hybrid zone between two chromosome races of the *Sceloporus grammicus* complex (Sauria, Phrynosomatidae). Evolution 49:48–60.

———, J. W. SITES, JR., AND I. F. GREENBAUM. 1992a. Chromosomal synapsis and the meiotic process in male mesquite lizards, *Sceloporus grammicus* complex. Genome 35:398–408.

———. 1992b. Synapsis, recombination, and meiotic

segregation in the mesquite lizard, *Sceloporus grammicus* complex. I. Pericentric inversion heteromorphism of the F5 cytotype. Cytogenet. Cell Genet. 61:40–45.

———. 1992c. Synapsis, recombination, and meiotic segregation in the mesquite lizard, *Sceloporus grammicus* complex. II. Fission heteromorphism of the FM2 cytotype and the evolution of chromosome 2. Cytogenet. Cell Genet. 61:46–54.

RZEDOWSKI, J. 1981. Vegetación de México. Editorial Limusa México. 432 pp.

SHAW, D. D., P. WILKINSON, AND D. J. COATES. 1983. Increased chromosomal mutation rate after hybridization between two subspecies of grasshoppers. Science 220:1165–1167.

SITES, J. W., JR. 1983. Chromosome evolution in the iguanid lizard *Sceloporus grammicus*. I. Chromosome polymorphism. Evolution 37:38–53.

———. 1993. Chromosomal variation in the *Sceloporus grammicus* complex (Sauria: Phrynosomatidae). Chromosomes Today vII:137–147.

———, N. H. BARTON, AND K. M. REED. 1995. The genetic structure of a mosaic hybrid zone between chromosome races of the *Sceloporus grammicus* complex (Sauria, Phrynosomatidae). Evolution 49: 9–36.

———, AND S. K. DAVIS. 1989. Phylogenetic relationships and variability within and among six chromosome races of *Sceloporus grammicus* (Sauria: Iguanidae) based on nuclear and mitochondrial markers. Evolution 43:296–317.

———, S. K. DAVIS, D. HUTCHISON, B. A. MAURER, AND G. LARA. 1993. Parapatric hybridization between chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae): structure of the Tulancingo transect. Copeia 1993:373–398.

SWOFFORD, D. L., AND R. B. SELANDER. 1989. Biosys-1: a computer program for the analysis of allelic variation in population genetics and biochemical systematics. Release 1.7. Illinois Natural History Survey, Champaign.

APPENDIX I

Specimens Examined

Sceloporus grammicus—N = 36. MEXICO: Hidalgo, 1.5 km W Santuario Mapethé (MZFC 5999-142–149); 0.3 km SE Santuario Mapethé (MZFC 5978-67–71, 5978-73–75, 5978-77–78, 5978-80–81, 5979-86, 5980-91, 5980-93, 5980-95–97, 5981-108–109, 5981-111); 0.35 km SE Santuario Mapethé (MZFC 5981-102–107, 5981-110).