

Divergence in the Island Night Lizard *Xantusia riversiana* (Sauria: Xantusiidae)

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INTRODUCTION

The island night lizard, *Xantusia riversiana* Cope (Fig. 1), is found only on Santa Barbara, San Clemente, and San Nicolas Islands off southern California (Fig. 2). The species is sufficiently divergent in morphology from its mainland relatives, *X. vigilis* Baird and *X. henshawi* Stejneger (Fig. 1), that it has been placed in the monotypic genus *Klauberina* by Savage (1957, 1963). Regardless of whether it is accorded generic (Savage 1957) or subgeneric (Bezy 1972) rank, *X. riversiana* is clearly more divergent than the other living vertebrates of the California Channel Islands, suggesting that it may have been present longer than other species on one or more of the islands. Moreover, casual observations indicate that there may be greater morphological differences between the island populations of *X. riversiana* than were documented by earlier work (Savage 1951, Smith 1946). In an effort to further clarify the evolutionary history of the species, we have compared electrophoretically determined genetic distances and divergence time estimates between the island populations with those between the species of *Xantusia*, and have reappraised inter-island differences in karyotypes, scalation, coloration, body size, clutch size, and variability.

MATERIALS AND METHODS

Two separate electrophoretic analyses were performed. In the first, 22 presumptive loci were scored for 15 *X. riversiana* from San Clemente Island, 15 from San Nicolas Island, and five from Santa Barbara Island. In the second study, 30 presumptive loci were analyzed for six *X. riversiana* from San Nicolas Island, six *X. riversiana* from San Clemente Island, six *X. henshawi* from the San Jacinto Mountains, and 20 *X. vigilis* from Antelope Valley, California (see Specimens Examined for exact localities). The procedures for preparing the gels, stains, and interpreting alleles follow Selander *et al.* (1971), with minor modifications (Yang *et al.* 1974, Kim *et al.* 1976).

The chromosomal methods utilized were described by Bezy (1972). Scalation was analyzed univariately with the BMDP3D program and multivariately by stepwise discriminant analysis (SDA) utilizing BMDP7M (Dixon 1975).

RESULTS

Electrophoresis

The 22-locus study indicated that 18 presumptive loci are fixed for identical electromorphs (alleles) in all three island samples. Polymorphisms were observed for MDH (San Nicolas Island), PGM-2 (San Clemente and Santa Barbara Islands), and GOT-2 and PGI (San Clemente and San Nicolas Islands) (Table 1). In the 30-locus study, identical alleles were fixed at 27 loci for San Clemente and San Nicolas; polymorphisms occurred for MDH-2 on San Nicolas and for ADH and PGM-2 on San Clemente (Table 2). Allele frequencies were used to compute genetic similarity and distance (Nei 1972). Inter-island genetic distances (Table 3) are, of course,



FIGURE 1. Living individuals of *Xantusia riversiana* (upper; San Clemente I.), *X. henshawi* (middle; LACM 127160; California: Riverside Co.: San Jacinto Mts., Snow Creek), and *X. vigilis* (lower; LACM 127154; Mexico: Durango: 6.5 mi NE Pedriceña).

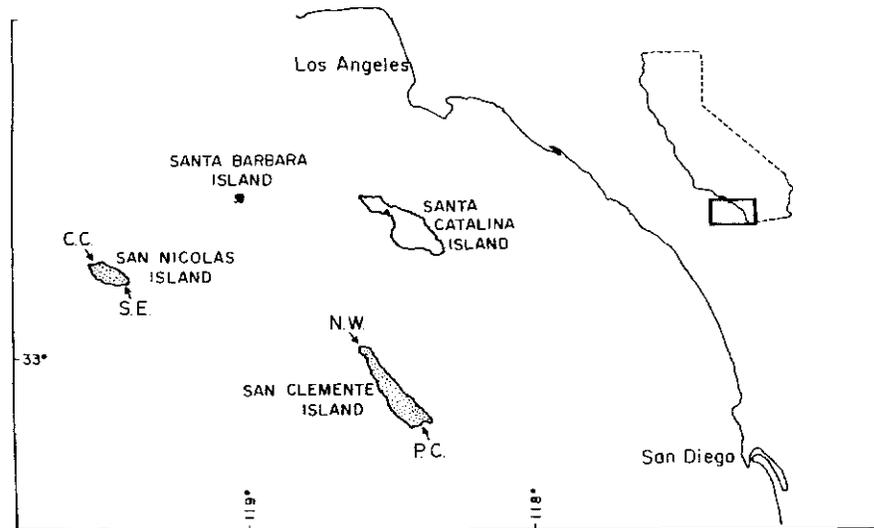


FIGURE 2. Distribution of *Xantusia riversiana* (three stippled islands). Arrows indicate specific populations sampled.

TABLE 1. Allelic frequencies at four presumed loci for three island populations of *Xantusia riversiana*. Excluded are 18 presumed loci fixed for electrophoretically identical gene products: GP-1, GP-2, GP-3, GP-4, LDH-1, LDH-2, IDH-1, IDH-2, ADH, Pept-1, Pept-2, ES, GOT-1, PGM-1, MPI, XDH, SDH, and IPO.

Locus	Allele	Island population (Sample size)		
		San Clemente (15)	San Nicolas (15)	Santa Barbara (5)
MDH	a	0	.067	0
	b	0	.033	0
	c	1.0	.900	1.0
PGI	a	.033	.036*	0
	b	.967	.964	1.0
GOT-2	a	.067	.033	0
	b	.933	.967	1.0
PGM-2	a	.167	0	.2
	b	.833	1.0	.8

* Sample size = 14.

extremely small, since identical alleles either predominate or are fixed at all of the loci studied electrophoretically. While genetic distance values are smallest between Santa Barbara and San Clemente Islands (0.0004) and largest between San Nicolas and Santa Barbara Islands (0.0024; Table 3), none differ significantly from zero.

Xantusia riversiana was compared with *X. vigilis* and *X. henshawi* in the 30-locus study (Tables 2 and 3). Fixed differences occur between *X. riversiana* and *X. vigilis* at 10 loci (Nei distance, $\overline{ND} = 0.574$), between *X. riversiana* and *X. henshawi* at 14 loci ($\overline{ND} = 0.830$), and between the two mainland species at 8 loci ($\overline{ND} = 0.409$).

Karyotypes

The chromosomes of lizards from Santa Barbara (1♀, 34 cells) and San Nicolas (1♂, 53 cells) appear identical in number, shape, and relative size to those described by Bezy (1972) for the population on San Clemente (Fig. 3). Utilizing nonbanding techniques, this karyotype also appears identical to that of eastern populations of *X. vigilis* and *X. henshawi* (Bezy 1972).

Scalation

From a total of 217 specimens, data were taken for the following seven scale characters: scales around body (SAB; transverse count of dorsal scales at midbody); gulars (G; longitudinal count along ventral midline from gular fold to postmentals); fourth toe lamellae (FTL; longitudinal count, ventral midline); femoral pores (FP; one leg); ventrals (V; longitudinal count along midline, excluding preanals); preanals (PA; number of enlarged scales along midline between vent and ventrals); preanal enlargement (PAE; sum of diameters of four largest preanals over sum of lengths of four midbody ventrals). These characters were chosen because previous studies suggest they vary geographically in species of *Xantusia* (Bezy 1967, Smith 1946, Webb 1970). Sexual dimorphism was not significant ($P \geq 0.05$) in the largest sample (San Clemente, NW, mottled; 20♂, 20♀), and the sexes were combined in subsequent analyses.

Univariate analysis indicates significant ($P < 0.05$) differences between islands for all seven characters, except for ventrals and preanals between Santa Barbara and San Clemente Islands (Table 4). Stepwise discriminant analysis indicates significant separation between island

TABLE 2. Allelic frequencies at 18 presumed loci for four populations of *Xantusia*. Excluded are 12 loci that were fixed identically in all four populations: LDH-1, LDH-2, IDH-1, IDH-2, α GPDH, MPI, PGI, IPO-1, FUM, LAP, AB-2, and AB-3.

Locus	Allele	Species, Population, Sample size			
		<i>riverstana</i> San Nicolas 6	<i>riversiana</i> San Clemente 6	<i>henshawi</i> San Jacinto 6	<i>vigilis</i> Little Rock 20
MDH-1	a	0	0	1.0	1.0
	b	1.0	1.0	0	0
MDH-2	a	.167	0	1.0	1.0
	b	.833	1.0	0	0
6PGDH	a	1.0	1.0	.083	0
	b	0	0	.917	1.0
XDH	a	0	0	1.0	0
	b	1.0	1.0	0	0
	c	0	0	0	1.0
ADH	a	1.0	.917	0	0
	b	0	.083	0	0
	c	0	0	1.0	0
	d	0	0	0	1.0
SDH	a	0	0	1.0	0
	b	1.0	1.0	0	1.0
PGM-1	a	0	0	1.0	1.0
	b	1.0	1.0	0	0
PGM-2	a	0	0	.25	.5
	b	0	.33	.75	.5
	c	1.0	.67	0	0
Pept-1	a	0	0	1.0	1.0
	b	1.0	1.0	0	0
ME	a	0	0	1.0	1.0
	b	1.0	1.0	0	0
HEXO	a	0	0	1.0	0
	b	1.0	1.0	0	1.0
AB-1	a	1.0	1.0	0	1.0
	b	0	0	1.0	0
ES-1	a	0	0	1.0	.9
	b	1.0	1.0	0	.1
ES-2	a	0	0	0	.925
	b	0	0	1.0	.075
	c	1.0	1.0	0	0
ES-3	a	1.0	1.0	0	1.0
	b	0	0	1.0	0
IPO-2	a	0	0	0	1.0
	b	1.0	1.0	1.0	0
ES-4	a	0	0	1.0	0
	b	1.0	1.0	0	1.0

TABLE 3. Mean heterozygosity (\bar{H}), per cent polymorphic loci (P), and genetic distances (lower left) and similarity (upper right) of Nei (1972) for five populations of *Xantusia*. Figures with asterisks (*) are derived from the 22-locus study (Table 1); those without are based on the 30-locus study (Table 2).

	\bar{H}	P	<i>riverstiana</i> SB	<i>riverstiana</i> SC	<i>riverstiana</i> SN	<i>vigilis</i>	<i>henshawii</i>
<i>riverstiana</i> SB	0.92*	4.5*	—	.9996*	.9976*	—	—
<i>riverstiana</i> SC	1.23*	13.6*	.0004*	—	.9983*	.5894	.4529
	2.87	6.8			.9952		
<i>riverstiana</i> SN	1.58*	9.1*	.0024*	.0017*	—	.5864	.4477
	1.15	3.4		.0048			
<i>vigilis</i>	2.59	10.2	—	.5287	.5338	—	.6931
<i>henshawii</i>	2.22	6.8	—	.7922	.8036	.3666	—

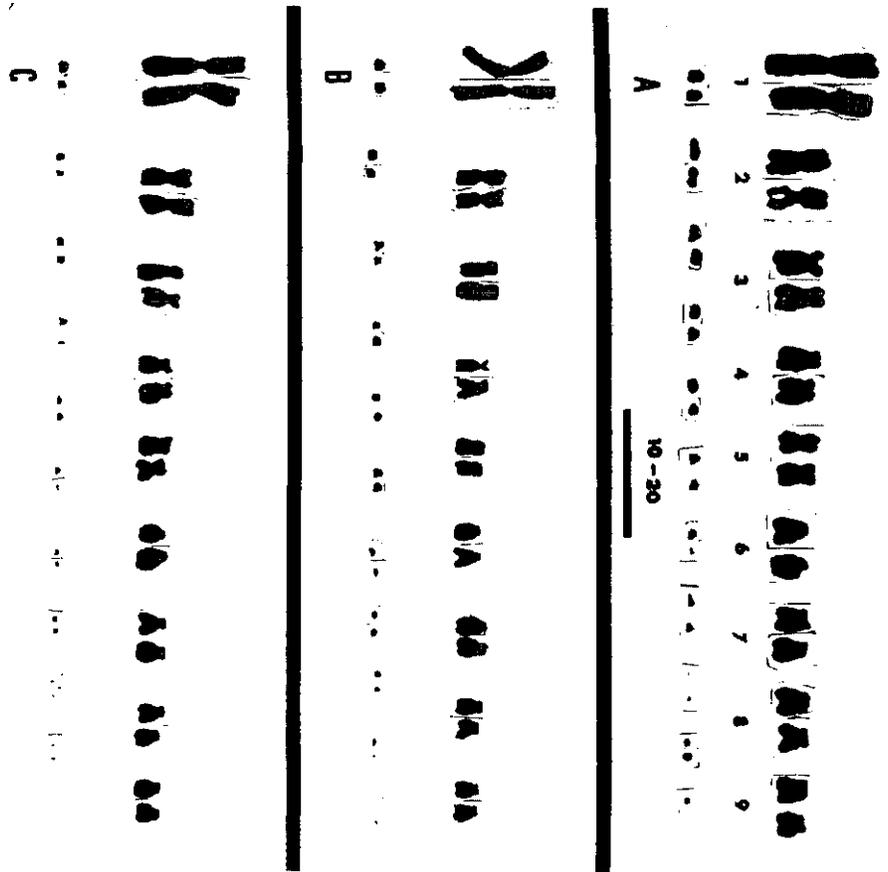


FIGURE 3. Karyotypes of individuals from three island populations of *Xantusia riversiana*: (A) San Clemente I., University of Arizona 21688, ♀; (B) San Nicolas I., LACM 127506, ♂; (C) Santa Barbara I., LACM 125465, ♀.

TABLE 4. Data for seven scale characters in nine samples of *Xantusia riversiana*. Mean \pm standard error (top line), range (middle line), coefficient of variation (bottom line), and sample size (below population) for scales around body (SAB), gulars (G), fourth toe lamellae (FTL), femoral pores (FP), ventrals (V), preanals (PA), and preanal enlargement (PAE) are given.

	SAB	G	FTL	FP	V	PA	PAE
Santa Barbara I.	84.15 \pm .48	50.47 \pm .46	23.28 \pm .06	11.23 \pm .09	34.00 \pm .16	4.98 \pm .10	123.64 \pm 2.29
40	79-92	43-58	22-25	10-12	32-37	4-6	105-167
	3.64	5.71	4.29	5.14	2.98	13.26	11.71
San Clemente I.	79.55 \pm .37	46.98 \pm .26	22.67 \pm .12	10.50 \pm .08	33.67 \pm .10	4.89 \pm .07	140.44 \pm 1.87
97	70-88	41-54	21-29	9-13	32-36	3-7	98-181
	4.57	5.44	5.39	7.66	2.90	13.82	13.08
San Nicolas I.	71.74 \pm .37	41.99 \pm .26	21.45 \pm .13	10.94 \pm .10	32.56 \pm .11	4.49 \pm .06	157.79 \pm 2.30
80	60-79	35-48	19-24	9-13	30-35	3-6	119-226
	4.56	5.64	5.29	8.01	3.12	12.78	13.06
San Clemente I.	81.25 \pm .79	47.15 \pm .69	22.20 \pm .22	10.45 \pm .15	33.95 \pm .20	5.00 \pm .10	129.80 \pm 3.25
Pyramid Cove	75-87	43-54	21-24	10-12	33-36	4-6	108-158
20	4.35	6.50	4.52	6.57	2.61	9.18	9.77
Northwest	78.65 \pm .40	46.91 \pm .30	22.70 \pm .17	10.46 \pm .13	33.50 \pm .12	4.73 \pm .09	148.98 \pm 2.11
57	70-86	42-52	21-29	9-12	32-36	3-7	114-181
	3.81	4.91	5.71	8.10	2.77	15.21	10.74
mottled	79.00 \pm .46	47.25 \pm .38	22.40 \pm .15	10.48 \pm .14	33.55 \pm .16	4.80 \pm .13	148.20 \pm 2.37
40	72-86	42-52	21-25	9-12	32-36	3-7	122-181
	3.70	5.13	4.27	8.37	2.94	16.48	10.12
striped	77.82 \pm .75	46.12 \pm .44	23.41 \pm .41	10.41 \pm .19	33.41 \pm .19	4.59 \pm .12	150.82 \pm 4.49
17	70-81	42-49	21-29	9-11	32-35	4-5	114-175
	3.97	3.90	7.25	7.64	2.38	11.06	12.27
San Nicolas I.	70.05 \pm .81	41.25 \pm .55	21.30 \pm .22	10.50 \pm .19	32.30 \pm .18	4.05 \pm .09	158.80 \pm 6.27
Carrier Cove	60-75	35-44	20-23	9-12	31-34	3-5	121-226
20	5.17	5.98	4.59	7.88	2.48	9.73	17.65
Southeast	72.75 \pm .47	42.15 \pm .33	21.87 \pm .18	11.23 \pm .15	32.77 \pm .17	4.60 \pm .08	159.10 \pm 2.67
40	67-79	37-48	20-24	9-13	31-35	4-6	128-214
	4.06	5.00	5.20	8.19	3.35	11.86	10.60

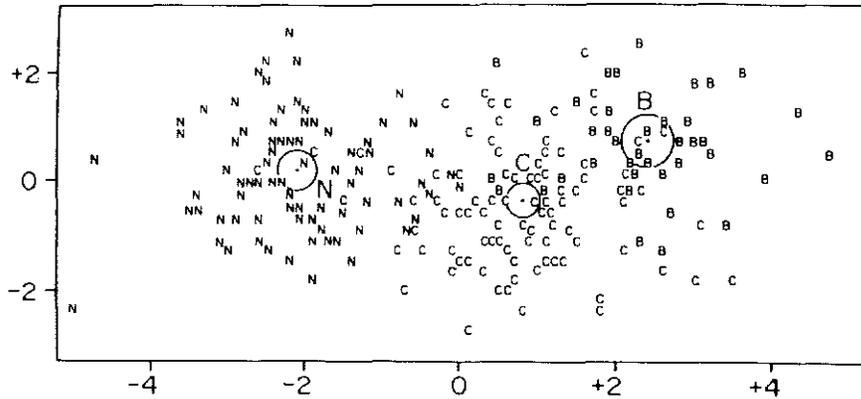


FIGURE 4. Plot of first two canonical variables separating the three island populations of *Xantusia riversiana*: (B) Santa Barbara I., 40 specimens; (C) San Clemente I., 97; and (N) San Nicolas I., 80. Population centroids (dots) are surrounded by 95 per cent confidence circles. The first variate (abscissa) represents 95 per cent of the observed variance.

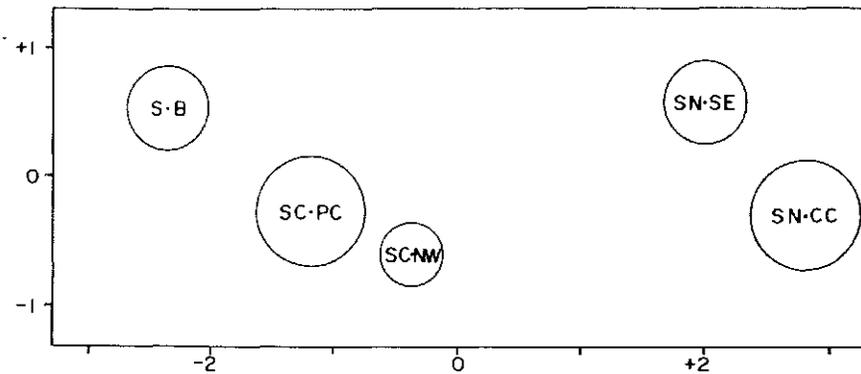


FIGURE 5. Plot of first two canonical variables separating five populations of *Xantusia riversiana*: Santa Barbara I. (SB); San Clemente I., Pyramid Cove (SCPC) and Northwest (SCNW); and San Nicolas I., Carrier Cove (SNCC) and Southeast (SNSE). Population centroids (dots) are surrounded by 95 per cent confidence circles. First variate (abscissa) represents 86 per cent of observed variance; second (ordinate), 7 per cent. See Figure 2 for location of populations.

TABLE 5. Inter-island comparisons of airline distance in km (AD), Mahalanobis' distance for scalation ($\sqrt{D^2}$), and genetic distance of Nei, 1972 (ND).

	AD	$\sqrt{D^2}$	ND
Santa Barbara-San Clemente	77	1.91	.0004
San Clemente-San Nicolas	101	2.95	.0017
San Nicolas-Santa Barbara	49	4.66	.0024

TABLE 6. Pooled standard deviations and canonical variate coefficients, with standardized scores in parentheses, for seven characters in the inter-island stepwise discriminant analysis.

	SD	I		II	
SAB	3.403	0.175	(0.596)	-0.025	(-0.085)
G	2.555	0.155	(0.396)	0.081	(0.207)
FTL	1.153	0.220	(0.254)	-0.044	(-0.051)
FP	0.797	-0.245	(-0.195)	1.116	(0.889)
PAE	18.621	-0.010	(-0.186)	-0.017	(-0.317)
V	1.000	0.180	(0.180)	-0.283	(-0.283)
PA	0.634	0.029	(0.018)	-0.586	(-0.372)

TABLE 7. Classification matrix based on stepwise discriminant analysis of 216 *Xantusia riversiana* from Santa Barbara (SB), San Clemente (SC), and San Nicolas (SN) Islands.

	Total	Per cent correct	Number of cases classified into group		
			SB	SC	SN
SB	39	87.2	34	6	0
SC	97	78.4	16	76	5
SN	80	91.2	0	7	73
Total	216	84.7	50	88	78

centroids (Fig. 4). As with the results of the electrophoretic analyses, the order of increasing divergence (Mahalanobis' distance, $\sqrt{D^2}$) was: San Clemente-Santa Barbara (1.91), San Clemente-San Nicolas (2.95), and Santa Barbara-San Nicolas (4.66) (Tables 5 and 6). The *a posteriori* classification scored 91 per cent hits for San Nicolas, 87 per cent for Santa Barbara, and 78 per cent for San Clemente. The classification matrix (Table 7) again emphasizes the intermediate position of San Clemente and its relative closeness to Santa Barbara in the discriminant space.

To test for intra-island geographic variation, samples were compared from two distant localities on both San Clemente (NW and Pyramid Cove) and San Nicolas (SE and Carrier Cove) (Fig. 2). Significant differences were found for SAB and PAE between the San Clemente populations, and for SAB, FP, and PA between the San Nicolas populations (Table 4). For both intra-island comparisons the centroids are significantly different (Fig. 5) and their

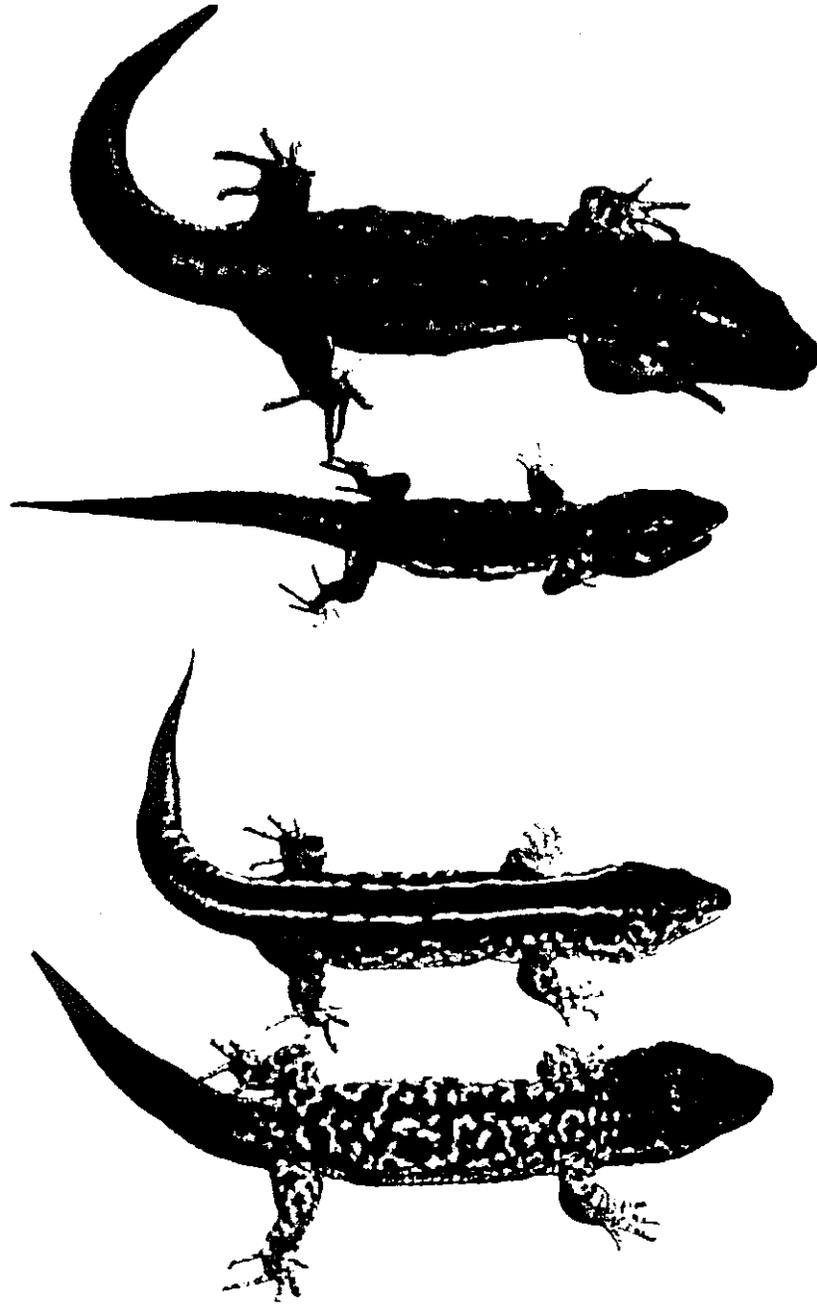


FIGURE 6. Living individuals of *Xantusia riversiana* from Santa Barbara I. (upper two; LACM 127128 and 108835) and San Clemente I. (lower two; LACM 108618 and 108619).

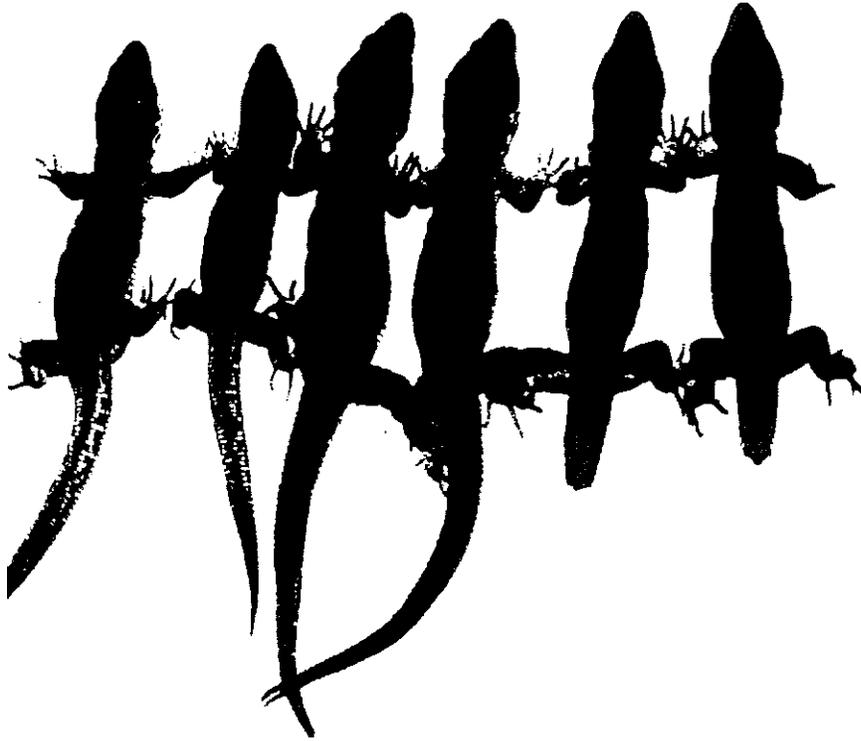


FIGURE 7. Living individuals of *Xantusia riversiana* from San Nicolas I. (LACM 108505 through 108509 and 108813).

Mahalanobis' distances are nearly identical (1.59 and 1.63) and are smaller than for all inter-island comparisons (2.07 to 5.43).

Color Pattern

Color pattern in *Xantusia riversiana* is highly variable (Figs. 6 and 7). Individuals with mottled patterns are found on all three islands; those with longitudinally striped patterns occur on San Clemente and San Nicolas, and a "blank" (uniform tan) pattern was observed only among San Nicolas lizards. There are, however, more subtle island differences in color pattern which we did not attempt to quantify, but which are illustrated in Figures 6 and 7. The color patterns of lizards from San Clemente tend to be more highly contrasting than those of individuals from Santa Barbara (Fig. 6). San Nicolas color patterns are the most variable and include striped, blank, and finely reticulated patterns, as well as many intermediates, often with reddish backgrounds (Fig. 7).

Scale counts were compared between striped and mottled individuals in the NW San Clemente population. Significant differences were detected only for fourth toe lamellae. The population centroids do not differ significantly and only 68 per cent hits were scored in the *a posteriori* classification of the SDA. The apparent association of color morphs with signifi-

TABLE 8. Clutch size from two sources for three island populations of *Xantusia riversiana*. Mean \pm standard error, range, and sample size.

	Santa Barbara	San Clemente	San Nicolas
Goldberg and Bezy (1974)	3.50 3-4 2	3.76 \pm .23 2-6 25	4.55 \pm .50 3-7 9
Brattstrom (1951)	— — —	4.80 \pm .37 4-6 5	7.50 \pm .65 6-9 4
Total	3.25* 3-4 4	4.03 \pm .20 2-6 30	5.46 \pm .55 3-9 13

* Includes two additional individuals (LACM 125466 and 125467), each with three enlarged eggs.

cant differences in FTL may be a result of minor geographic variation, as the NW San Clemente sample was collected over a 6.5-km² area (Goldberg and Bezy 1974) and local "pockets" of striped individuals were noted in collecting the samples.

All three color morphs occur in mainland populations of *Xantusia vigilis*.

Body Size

The means for snout-vent lengths (SVL) of specimens 75 mm or longer (size at maturity for San Clemente females; Goldberg and Bezy 1974) are: Santa Barbara, 83.35 \pm 1.31 (n = 31); San Clemente, 84.24 \pm 0.42 (n = 294); and San Nicolas, 88.85 \pm 0.80 (n = 86). The differences are significant, except for Santa Barbara vs. San Clemente.

Adult *Xantusia riversiana* (SVL = 65 to 109 mm; Goldberg and Bezy 1974) are considerably larger than their mainland relatives *X. vigilis* (SVL = 36 to 60 mm; Bezy 1967, Zweifel and Lowe 1966) and *X. henshawi* (SVL = 47 to 70 mm; Lee 1975) and have been cited as an example of insular gigantism (Carlquist 1965). Large body size may be a primitive character state for xantusiids, retained by *X. riversiana*, and is perhaps associated with a herbivorous diet (Brattstrom 1952, Mautz and Lopez-Forment 1978, Pough 1973, Regal 1968).

Clutch Size

Brattstrom (1951) and Goldberg and Bezy (1974) have presented data on clutch (= litter) size in *X. riversiana* (Table 8). The figures reported by Brattstrom (1951) are considerably higher than those of Goldberg and Bezy (1974), perhaps reflecting annual variations in clutch size. Clutch size is smallest for Santa Barbara Island and largest for San Nicolas Island in both sets of data, but because of sample size limitations the accepted level of significance is achieved only for San Clemente vs. San Nicolas, and only when the two sets of data are pooled.

While a correlation between body size and clutch size was not present in the population on San Clemente (Goldberg and Bezy 1974), it appears to hold for comparisons between island populations. This correlation may also hold for the family in general since clutch size in *X. riversiana* is clearly larger than in its smaller mainland relatives *X. vigilis* (\bar{x} = 1.87; Zweifel and Lowe 1966) and *X. henshawi* (\bar{x} = 1.46; Lee 1975), but similar to that of comparably sized species of *Lepidophyma* (4 to 8; Telford and Campbell 1970, Greene 1970).

TABLE 9. Comparison of eight phenotypic and genotypic characteristics and seven ecogeographical parameters for the three island populations of *Xantusia riversiana*. Color pattern classes are mottled (M), striped (S), and blank (B). Data for last seven parameters (except lizard species number) are from Power (1972).

	Santa Barbara	San Clemente	San Nicolas
Canonical axis I	2.21	0.66	-1.93
Snout-vent length (\bar{X} , mm)	83.35	84.24	88.85
Clutch size (\bar{X})	3.25	3.76	4.55
Color pattern	M	M, S	M, S, B
Coefficient of variation (\overline{CV}_1)	4.35	5.19	5.32
Coefficient of variation (\overline{CV}_2)	4.35	4.99	5.19
Heterozygosity (\bar{H})	0.9	1.2	1.6
Area (km ²)	2.6	145	36
Elevation (m)	194	599	253
Latitude (°N)	33.4	32.9	34.0
Mainland distance (km)	61	79	98
Island distance (km)	126	178	150
Plant species number	40	235	190
Lizard species number	1	2	1 (+2?)

Variability

The mean coefficients of variation (\overline{CV}) of five scale characters for the island populations are given in Table 9. In computing \overline{CV} , PA and PAE were not included because of their unusually high level of variability ($\overline{CV} = 13.29$ and 12.62 , respectively). The order of increasing \overline{CV} of the island populations is Santa Barbara, San Clemente, and San Nicolas, whether \overline{CV} for San Nicolas and San Clemente is computed as the average of the \overline{CV} 's of their respective intra-island populations (\overline{CV}_1), or from the pooled standard deviation for the entire island sample (\overline{CV}_2) (Table 9). In comparison with mainland species, *X. riversiana* does not appear to have reduced scale count variability; \overline{CV} for four characters (SAB, FTL, G, and FP) in *X. vigilis* (Bezy 1967) is 5.40, as opposed to 5.47 for *X. riversiana*.

For the 22-locus study, the heterozygosity (\bar{H}) figures correspond well to \overline{CV} values, Santa Barbara Island being the least and San Nicolas Island the most variable (Table 3). These data might seem to support the genetic-phenetic variation correlation demonstrated by Soulé *et al.* (1973) for insular *Anolis* and deep-water island populations of *Uta*, and by Patton *et al.* (1975) for Galapagos *Rattus*. That such a correlation exists for *X. riversiana* must, however, remain questionable because the number of islands sampled is necessarily limited to three, our electrophoretic sample sizes are small (20, 20, and 5), and the results of the 30-locus study are contradictory, indicating instead that the larger San Clemente is genetically more variable than the smaller San Nicolas.

Electrophoretic estimates of genetic variability in the two mainland species are similar to those of the island populations (Table 3). All populations of *Xantusia* sampled have low heterozygosity values ($\bar{H} \approx 2.21$, 30 loci) when compared with other vertebrates (Selander and Kaufman 1973). Gorman *et al.* (1977) compared heterozygosity estimates for 10 genera of lizards and concluded that the values are low (*ca.* 2 per cent) in fossorial species, intermediate (*ca.* 5 per cent) in territorial, sit-and-wait predators, and high (*ca.* 10 per cent) in vagile,

searching predators. These categories presumably influence heterozygosity values through territoriality, population size, and/or mating structure (degree of panmixia).

The heterozygosity levels of *Xantusia* are comparable to those of fossorial species, which these lizards resemble in that they are sedentary, live (often paired) in patchy habitats (e.g., boulder cap rocks and yuccas), and have long lives and low reproductive potentials (Bezy *et al.* 1977, Goldberg and Bezy 1974, Lee 1975, Zweifel and Lowe 1966).

DISCUSSION

Ecological Correlates

That our studies of *X. riversiana* are necessarily limited to three islands precludes any detailed analysis of correlations between the data and island ecological parameters. However, we briefly consider here possible ecological correlates only because a consistent order (Santa Barbara-San Clemente-San Nicolas) occurs in our data for genetic distance, scalation, color pattern, body size, clutch size, heterozygosity, and scale count variability (Table 9). This order contradicts that for island area, elevation, latitude, plant species number, and lizard species number, but corresponds with mainland distance (Table 9; Power 1972). Mainland distance could have affected colonization sequence, which may be reflected in the electrophoretic data. However, for at least scalation, body size, and clutch size, it is likely that the observed pattern of variation is related to climatic factors which are correlated with mainland distance. Other studies have demonstrated that with island area there is a significant negative correlation for dorsal scale number and body size in *Uta* (Soulé 1966), and significant positive correlations for both phenetic and genetic variability in *Uta* (Soulé 1972, Soulé and Yang 1973) and in *Rattus* (Patton *et al.* 1975). None of these parameters appears correlated with island area in our data; plausible explanations for this include the small number of islands, the relatively near-shore position of the islands, the recency of colonization, and possible differences in response to environmental variables related to the secretive lifestyle of xantusiids.

Evolution and Biogeography

On the basis of correlations between electrophoretic data, immunological distance, and the fossil record, Sarich (1977) has estimated that a genetic distance of 1.0 (Nei 1972) indicates a divergence time of approximately 18 million years (m.y.) ago. This correlation would predict that *Xantusia riversiana* diverged from *X. henshawi* about 15 m.y. ago (middle Miocene) and from *X. vigilis* about 10 m.y. ago (late to middle Miocene), while the divergence time between the two mainland species would be approximately 7 m.y. ago (late Miocene).

Schatzinger (1975) has recognized two species of *Paleoxantusia* from the later Eocene (Uintan) of the San Diego region, the larger one sharing characters with *X. riversiana* and the smaller one with *X. henshawi* and *X. vigilis*. The presence of these *Paleoxantusia* species in the Uintan would seem to suggest that the cladistic event that led to *X. riversiana* and *X. henshawi-vigilis* took place over 40 m.y. ago. However, after extensive comparisons among fossil and recent xantusiids, Schatzinger (1975, fig. 9) concluded that these two *Paleoxantusia* species do not represent the divergence between *X. riversiana* (*Klauberina*) and *X. henshawi-vigilis* (*Xantusia*), which he feels took place in the Oligocene or later. Our divergence time estimates based on electrophoretic data support his conclusion.

The genetic distances between the island populations are extremely small compared with those between the species, indicating that at least two, if not all three, of the present island populations are the result of colonization in the last million years. One of the three could conceivably have been in existence for 10 to 14 m.y., the divergence time between *X. riversiana* and its living mainland relatives.

The electrophoretic data appear consistent with the known geological record of the islands (as summarized by J. Vedder, pers. comm.). Pleistocene marine deposits occur on all three islands. On San Nicolas, these are found to the highest present elevation (253 m) and have been estimated to be 0.5 to 0.6 m. y. old. Pleistocene beds that are probably marine cover the highest point (194 m) on Santa Barbara Island, and fossiliferous marine beds occur at the next lower terrace. On San Clemente Island, however, the record of Pleistocene submergence is not as complete. Pleistocene marine beds and wave-cut terraces occur to an elevation of approximately 450 m, leaving 149 m without a conclusive record of Quaternary submergence. Miocene and Pliocene marine beds also occur on San Clemente. While the geological history of the California borderland is highly complex, the evidence would seem to indicate that the colonizations of San Nicolas and Santa Barbara must have been Quaternary events, while it is possible that colonization on San Clemente dates from the late Tertiary.

The occurrence of *X. riversiana* on islands with records of Pleistocene submergence which were not connected by land bridges suggests that the species is at least a moderately effective island colonizer. The recent discovery of the species on Sutil Island off the north end of Santa Barbara Island (R. Wilson, pers. comm.) strengthens this idea. In contrast, *X. vigilis* occurs on none of the islands of the Gulf of California, in spite of its circumgulf distribution, and appears to lack all of the life history attributes that are correlated with successful Gulf island colonization among species of lizards, i.e., habitat generalists having high mainland population densities, potentially high birth rates, and high death rates (Case 1975).

The differences in apparent colonizing abilities between the two species seem consistent with what is known of their ecology and life history. The clutch size of *X. riversiana* is two to three times that of *X. vigilis* (Goldberg and Bezy 1974). The diet of *X. vigilis* consists almost exclusively of insects, while *X. riversiana* is a food generalist, its diet being about evenly divided between plant and animal material (Brattstrom 1952). Although *Xantusia vigilis* achieves high densities in relatively cool desert situations, such as in the Mojave (Zweifel and Lowe 1966) and at localities in Baja California receiving Pacific breezes, it is virtually absent from the hot Gulf coast of Sonora and Baja California (Bezy, pers. obs.). That it does not occur on the Gulf islands is not surprising. While *X. riversiana* no longer occurs on the mainland, its fossil relatives (*Paleoxantusia*) appear to have had a long association with the maritime climates of the California borderland (Schatzinger 1975), and today the species reaches high population densities on at least San Clemente Island (Wilson 1976). It is probably the differences in climate, rather than population parameters, that explain the absence of *X. vigilis* on the Gulf islands and the presence of *X. riversiana* on the California Channel Islands.

One of the more interesting unanswered (and perhaps unanswerable) questions posed by *X. riversiana* is why it does not occur today on the mainland or on other California Islands. Insular shielding from competition, predation (Savage 1967), and harsh climatic factors (Regal 1968) have all been suggested, and with good reason. Compared with *X. henshawi* and *X. vigilis*, the species is morphologically unspecialized (Savage 1967) and its large body size limits its habitat and thermoregulatory options (Regal 1968). All three islands lack snakes as potential predators (Savage 1967), two have no other native lizard species, and San Clemente has only *Uta stansburiana*. (Records for *Uta stansburiana* [Savage 1967] and *Gerrhonotus multicarinatus* [Banta and Wilson 1976] on San Nicolas probably represent introductions.)

However, competition may not have played an important role in the elimination of *X. riversiana* from the mainland or islands since no other extensively herbivorous lizard is known from the California borderland, at least for the Quaternary. The secretive habits of the species would be expected to minimize predation, except by snakes, and it seems unlikely that predation from this source alone could have been a large factor in bringing about extinction. It

would appear more reasonable that climatic change has played the dominant role in producing the relictual biogeographic pattern exhibited by several xantusiids, including *X. riversiana* (Bezy 1972). The species has probably persisted on the islands primarily because the greater equability of climate there has offered a substantial buffer against the climatic deteriorations of the Neogene. Among the California Islands, the outer, southern ones would be expected to offer the maximum climatic buffer, and it is to these that *X. riversiana* is restricted. That the mainland extinction of the species may have occurred more than one million years ago is suggested by the general fossil record for mainland North America (north of the Isthmus of Tehuantepec), which indicates virtually no extinction of lizard species since Blancan times (Gehlbach 1965).

In summary, the available evidence suggests that the divergence between *Xantusia riversiana* and *X. henshawi-vigilis* took place in the Miocene. *Xantusia riversiana* could have occurred on San Clemente Island as early as the late Miocene or Pliocene, and its disappearance from the mainland may date to pre-Nebraskan times. In the last half million years or so the species has reached San Nicolas and Santa Barbara Islands, perhaps from San Clemente Island, and the resultant populations have become differentiated in scalation, coloration, body size, and clutch size.

SPECIMENS EXAMINED

Catalogue numbers refer to specimens in the collections of the Los Angeles County Museum of Natural History (acronym, LACM, omitted), the Museum of Vertebrate Zoology (MVZ), and the San Diego Natural History Museum (SDNHM). All localities are in California. Santa Barbara Island is in Santa Barbara County, San Clemente Island in Los Angeles County, and San Nicolas Island in Ventura County.

(A) Electrophoresis.

X. henshawi: RIVERSIDE CO.: ca. 1.3 mi (by road) S Cabezon, 125524-29.

X. vigilis: LOS ANGELES CO.: 3.5 mi (airline) W Littlerock, 125530-49.

X. riversiana: SANTA BARBARA I.: vic. Cat Canyon, 125463-67. SAN CLEMENTE I.: vic. dunes, NW side of I., 125470-83, 125506-10; 4.8 mi (airline) SE Wilson Cove, 125468; Horse Cove, 125469. SAN NICOLAS I.: Carrier Cove, SE of W Point, 125486-505; beach along SSE side of I., 125512.

(B) Karyotypes.

SANTA BARBARA I.: vic. Cat Canyon, 125465. SAN NICOLAS I.: beach along SSE side of I., 127506.

(C) Scalation.

SANTA BARBARA I.: 3278-85, 3287-88, MVZ 644-45, MVZ 28330, SDNHM 21128, SDNHM 31983-85, SDNHM 44469; vic. Cat Canyon, 108822-38, 125463-67. SAN CLEMENTE I.: *NW Sample*, vic. airport, 108306, 108309-11, 108315, 108319-20, 108322-23, 108327, 108330, 108336, 108347, 108352-56, 108359, 108362-63, 108371-72, 108446, 108449, 108451, 108455-56, 108459, 108462-64, 108470, 108473, 108483-84, 108486-89, 108495-97, 108499-500, 108504, 108563, 108577, 108588, 108618, 108620, 108646, 108654, 108678, 108709, 108734, 108739. *Pyramid Cove Sample*, 3309, 3317, 3330, 3368-69, 3371, 3373, 3377-81, 3383, 3387, 3389-90, 3392-94, 3401. *General Sample*, Mt. Thirst, 119174; Middle Ranch, 26798; Horse Cove, 125469; ca. 3 mi W Pyramid Cove, 108607-16; 4 mi S Wilson Cove, 101255-59; 5 mi E Wilson Cove, 101254; 4.8 mi (airline) SE Wilson Cove, 125468. SAN NICOLAS I.: *SE Sample*, 108769-74, 108777-88, 108791, 108793-800, 108802, 108804-09, 108811-12, 108818, 125512-14. *Carrier Cove*

Sample, SE of W Point, 121670-71, 122572, 125486-94, 125496, 125498, 125501-05, 125511. General Sample, 3267, 14487, 101262, SDNHM 15487-92, SDNHM 15494-5, SDNHM 17213, SDNHM 17215, SDNHM 36334, SDNHM 36670-71; Army Camp, 3266; Sand Dunes, 3275-77.

SUMMARY

Xantusia (Klauberina) riversiana is endemic to Santa Barbara, San Clemente, and San Nicolas Islands. Electrophoretic analyses of proteins encoded by 22 to 30 presumptive loci indicate that the genetic distances between the island populations are minute ($ND = 0.0004$ to 0.0048), compared with those between the species of *Xantusia* (0.409 to 0.830), and that the heterozygosity levels are low in all the populations ($\bar{H} = 1.80$). The unbanded karyotypes of the three island populations appear identical to each other and to those of certain populations of both mainland species. Stepwise discriminant analysis of seven characters demonstrates both intra-island and inter-island divergence in scalation, with an average of 85 per cent of the specimens being correctly assigned to their home island. The island populations have also diverged in coloration, body size, and clutch size. Electrophoretic data suggest that the divergence time between *X. riversiana* and *X. henshawi-vigilis* is 10 to 15 m.y. ago (ca. middle Miocene), while that between the island populations is less than one m.y. ago. *Xantusia riversiana* could have occurred on San Clemente island from as early as the Miocene or Pliocene and its disappearance from the mainland may date from pre-Nebraskan time.

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