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A New Lizard Species in the Genus *Xantusia* from Arizona

By

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ABSTRACT Three species of lizards in the genus *Xantusia* occur in Arizona: *X. vigilis*, *X. arizonae* and a new species described here, *X. bezyi*. Previous workers have suggested that only a single species of *Xantusia* is found in Arizona with some populations living in yucca-type plants and others specializing in granite rock habitats. Recognition of the three species is based on previously reported allozyme data, new mitochondrial DNA sequence data (1716 aligned sites, 59 parsimony informative), and morphological differences. Phylogenetic analysis of mitochondrial DNA sequences among the three species of *Xantusia* that occur in Arizona indicate that *X. arizonae* and *X. vigilis* are sister taxa with the exclusion of *X. bezyi*. Genetic differentiation between mitochondrial DNA sequences suggests that species in Arizona are 5–6 million years old.

Key Words: Reptilia; Squamata; Xantusiidae; *Xantusia*; new species; systematics; phylogenetics; mitochondrial DNA; Arizona.

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INTRODUCTION

The lizard genus *Xantusia* currently consists of five species: *X. bolsonae* in Durango, Mexico, *X. henshawi* in southern California and Baja California Norte, Mexico, *X. riversiana* on three of the California Channel Islands, *X. sanchezi* in southwestern Zacatecas, Mexico, and *X. vigilis* with seven subspecies occurring in California, Nevada, Utah, and Arizona in the United States and in Baja California, Sonora, Durango, and Zacatecas in Mexico (Bezy and Flores Villela, 1999).

Xantusia arizonae was described by Klauber (1931) from the vicinity of Yarnell in Yavapai County, Arizona. The lizards were found under flakes of granite boulders in a habitat similar to that of *X. henshawi* in southern California. *Xantusia arizonae* was diagnosed as being similar in lepidosis and partly in color and pattern to *X. vigilis* but with a body form more like that of *X. henshawii* but with relatively longer limbs and a more flattened head and body than *X. vigilis*. At the time of Klauber's (1931) discovery, the nearest known localities for *Xantusia* were for *X. vigilis*, some 250 km northwest in the eastern Mojave Desert.

For the next 35 years *Xantusia arizonae* was treated as a full species (Savage, 1963; Stebbins, 1954, 1966). Stebbins (1954) in his key to the species of *Xantusia*, distinguished *X. arizonae* from *X. vigilis* with the former having more subdigital lamallae on the fourth toe (25–28 versus 18–21) and more dorsal granular scales at midbody (43–50 versus 33–40).

Additional populations of granite-adapted lizards have been found in Arizona along the southwestern edge of the Colorado Plateau across a 300-kilometer region from near Valentine in Mojave County to the Superstition Mountains in Pinal County. Yucca-dwelling populations assigned to *X. vigilis* are also known from Arizona. Populations of *X. vigilis* and *X. arizonae* have been found within 50 km of each other in Yavapai County, Arizona. At one site near Tonto National Monument in Gila County, Arizona, Bezy (1967b) found both granite- and yucca-dwelling *Xantusia* together. There is an ecologically based morphological gradient from a "granitoform" to a "yuccaform" morphotype (Bezy, 1967b).

Bezy (1967b) noted that the "granitoform" occurred in two widely separated places, the southwestern edge of the Mogollon Rim of Arizona and the western foothills of the southern Sierra Nevada of California. The latter had just been described as *X. vigilis sierrae* (Bezy, 1967a). Bezy (1967b) found extensive morphological gaps between the most divergent populations of "granitoform" versus "yuccaform," but in all characters examined, these gaps were spanned by the ranges of variation of morphologically intermediate populations. He recommended that *X. arizonae* be treated as a subspecies of *X. vigilis*. This taxonomic arrangement was generally accepted (Crother et al., 1986; Stebbins, 1985; Webb, 1970).

In their discussion on species relationships Bezy and Sites (1987:288) concluded: "Before phylogenetic relationships among the species of *Xantusia* can be fully assessed with allozymes, additional data for populations of *X. vigilis* are needed, as the genetic and cladistic diversity within this apparently paraphyletic taxon is at least as great as among the presently recognized species units." Bezy and Sites (1987) reported data for three presumptive populations of *X. vigilis arizonae* which consistently appeared in three separate positions on their phylogenetic trees.

We present new mitochondrial DNA evidence and examine previously reported allozyme data (Bezy and Sites, 1987) to ascertain phylogenetic relationships and the extent of differentiation among populations of *Xantusia* occurring in different ecological habitats in Arizona. Under the phylogenetic species concept (Cracraft, 1989), these data suggest the occurrence of more than one species in Arizona. We conclude that three species of *Xantusia* occur in Arizona. They are *X. vigilis*, *X. arizonae*, and the new species described here. This new species lives in crevices in granite boulders (Fig. 1). It was previously regarded as a population of *X. arizonae* (Bezy and Sites, 1987).

ACKNOWLEDGMENTS

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MATERIALS AND METHODS

Museum numbers and localities for voucher specimens from which DNA was extracted, and GenBank accession numbers are presented below. Museum numbers and localities for voucher specimens examined morphologically are listed in the species description. Institutional codes are: KU = Natural History Museum, University of Kansas; MVZ = Museum of Vertebrate Zoology, University of California at Berkeley. Localities of voucher specimens are reported exactly as recorded in museum records and therefore may be expressed either in English or met-

Fig. 1. Type locality of *X. bezyi*, elev. 948 m, 33° 49.48′ N, 111° 28.55′ W, NE 1/4 Sec. 31, T. 6 N., R. 9 E., 5.6 km S (by Highway 87) of Sunflower, Maricopa County, Arizona.

ric units. Measurements were taken using dial calipers (to the nearest 0.1 mm). The description of scale characters follows the standard terminology used by Savage (1963) and Bezy and Flores Villela (1999). Photos of live *Xantusia* were taken on granite from the localities where they were collected.

Tissues were collected and directly stored in freezers (–80 C) until used. Four samples of *Xantusia* were sequenced: *X. henshawi*, MVZ 229092, AF404750, elev. 3000 ft., NW 1/4 Sec. 36, T. 6 S., R. 5 E., junction of Carrizo Road and Highway 74, 12.2 miles south of Palm Desert on Highway 74, Riverside County, California; *X. bezyi*, MVZ 232604, AF404751, elev. 914 m, 33° 49.48′ N, 111° 28.55′ W, NE1/4 Sec. 31, T. 6 N., R. 9 E., 5.7 km south (by Highway 87) of Sunflower, Maricopa Coounty, Arizona; *X. arizonae*, MVZ 230599, AF404752, 1.5 miles south (airline) of Yarnell, Yavapai County, Arizona; *X. vigilis*, MVZ 228254, U71328 (Macey et al., 1997), elev. 5800 ft., SW 1/4 Sec. 14, T. 8 N., R. 12 E., Granite Mountains Plateau, Granite Mountains, San Bernardino County, California.

The mitochondrial gene region of ND1 (subunit one of NADH dehydrogenase), $tRNA^{Ile}$, $tRNA^{Gln}$, $tRNA^{Met}$, ND2, $tRNA^{Trp}$, $tRNA^{Ala}$, $tRNA^{Asn}$, $tRNA^{Cys}$, $tRNA^{Tyr}$, and COI (subunit one of cytochrome *c* oxidase) was sequenced. Sequencing protocols follow Macey et al. (1997) except that cycle-sequencing reactions were run on an ABI Prism Big Dye Terminator DNA Sequencing Kit (Perkin-Elmer) with a denaturation at 95°C for 15 sec, annealing at 50°C for 1 sec, and extension at 60°C for 4 min for 35–40 cycles. Sequencing reactions were run on Long Ranger sequencing gels for 5–12 hours at 38-40°C and ABI 373 or MJ Research Basestation sequencers. The four sequences were aligned as 1716 sites (59 parsimony informative). A single gap was placed after the following positions in each sequence to obtain the alignment used in phylogenetic analyses: *X. henshawi*, 84, 1344, 1496, 1608; *X. bezyi*, 1544; *X. arizonae*, 1543; and *X. vigilis*, 1543.

Phylogenetic relationships were estimated using PAUP beta 4.0b3a (Swofford, 2001). Bootstrap resampling was used to assess support with 1000 replicates using exhaustive searches. The decay index was calculated by running searches that retained suboptimal trees using exhaustive searches. Alternative phylogenetic hypotheses were evaluated with the Wilcoxon signed-ranks test using the two-tailed probabilities (Felsenstein, 1985; Templeton, 1983). The allozyme analysis on the number of fixed differences between samples of *Xantusia* was derived from Table 2 in Bezy and Sites (1987).

DESCRIPTION OF NEW SPECIES

*Xantusia **bezyi***, new species

Holotype.—Museum of Vertebrate Zoology, MVZ 232604. An adult male from 33° 49.48′ N, 111° 28.55′ W, NE 1/4 Sec. 31, T. 6 N., R. 9 E., 5.6 km S (by Highway 87) of Sunflower, elev. 948 m, Maricopa County, Arizona, USA; found under an exfoliating granite slab on November 3, 2000 by Theodore J. Papenfuss.

Fig. 2. Adult male *Xantusia bezyi*, MVZ 232608, SVL 53.1 mm. Note that the color pattern is more similar to that of *X. henshawi* (Fig. 3) than to that of *X. arizonae*, (Fig. 4).

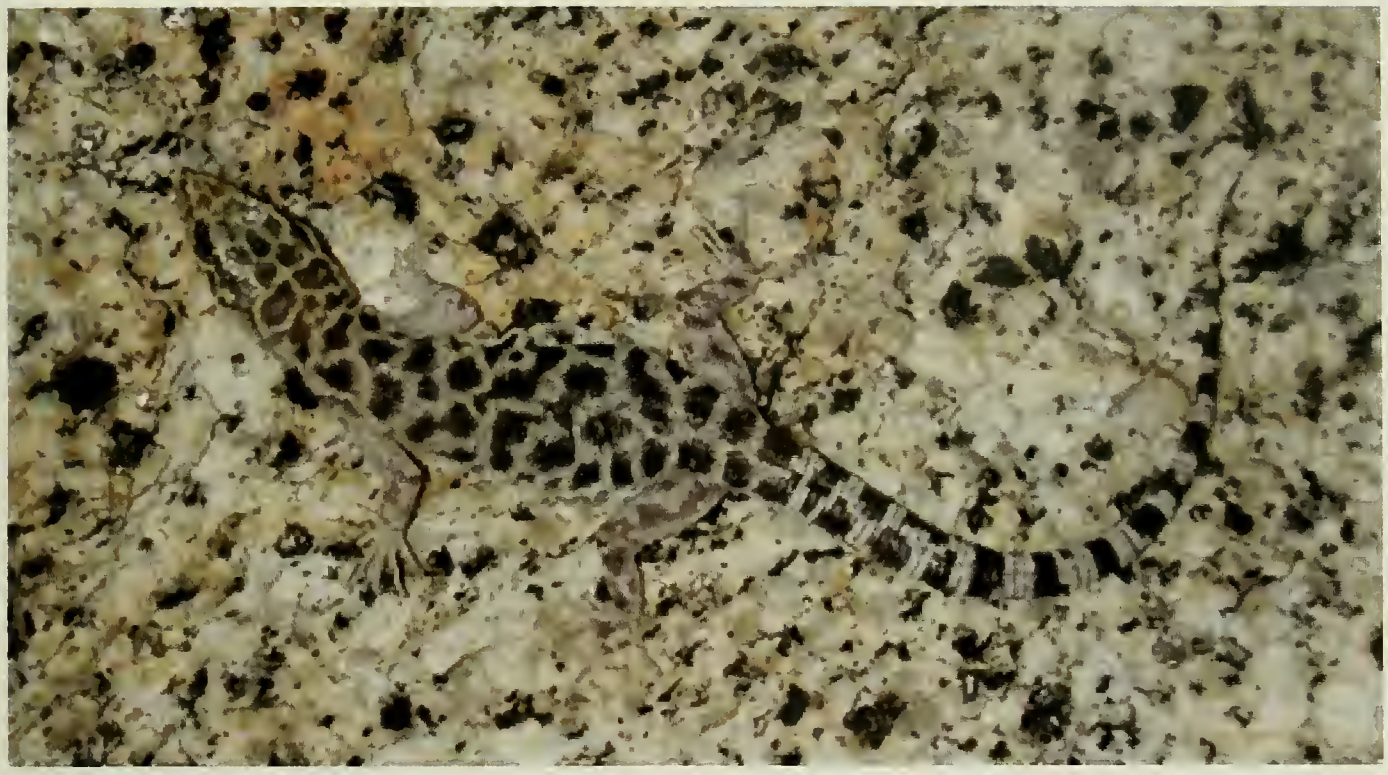

Fig. 3. *Xantusia henshawi*, MVZ 232630, SVL 58.3 mm, from 33° 31.18′ N, 116° 52.18′ W, 3.2 km SSE (by Wilson Valley Road) of junction with Sage Road, elev. 815 m, Riverside County, California.

Fig. 4. *Xantusia arizonae*, MVZ 232578, SVL 52.9 mm, from Yarnell, Yavapai County Arizona.

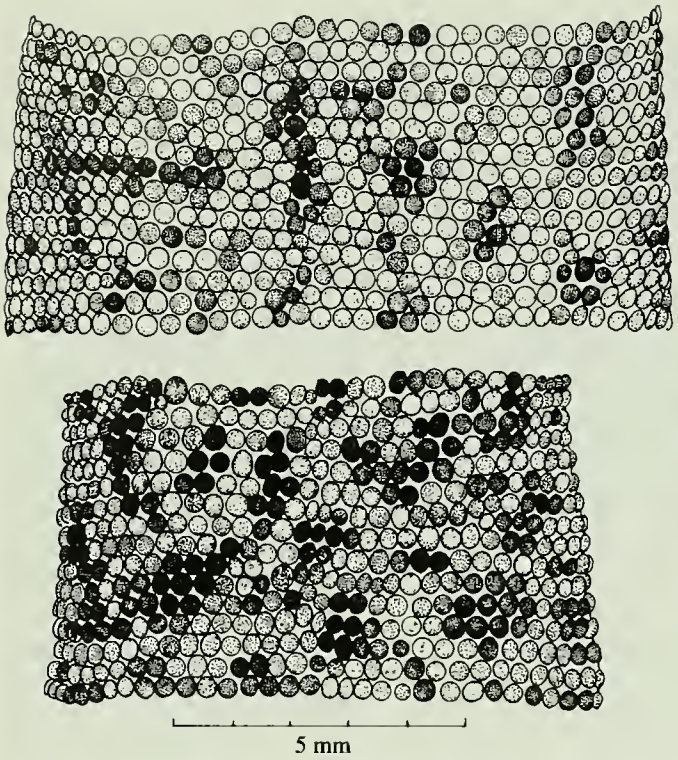

Fig. 5. Dorsal midbody color pattern. Above: *Xantusia arizonae*, MVZ 73829. The dark blotches seen here and in figure 4 consist of 4–12 individual dark granular scales. Below: *X. bezyi* holotype, MVZ 232604. The dark blotches seen here and in figure 2 consist of 3–28 individual dark granular scales.

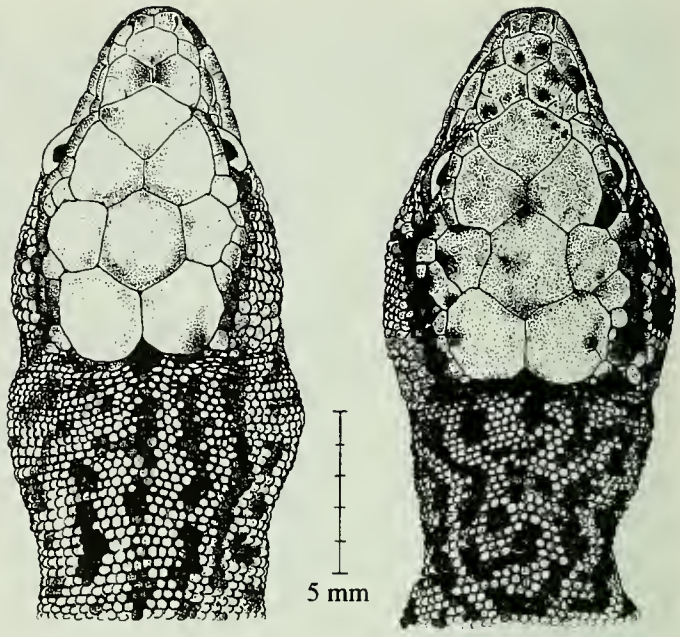

Fig. 6. Dorsal views of heads. Left: *Xantusia arizonae*, MVZ 73829. Right: *X. bezyi* holotype, MVZ 232604.

Paratypes.—Ten specimens. MVZ 232605–232607; from the type locality. MVZ 232608–232611, 232571; KU 290503–04 from 33° 51.10′ N, 111° 28.28′ W, NW 1/4 Sec. 29, T. 6 N., R. 9 E., 2.9 km S (by Highway 87) of Sunflower, elev. 1085 m, Maricopa County, Arizona, USA.

Diagnosis.—A moderately large (to about 58 mm snout-vent length) species of *Xantusia* that is similar in size and morphology to *X. arizonae*. It differs from the latter in allozymes, mitochondrial DNA, and color pattern. The dorsal blotches of adults (Fig. 2) are more similar to the pattern in *X. henshawi* (Fig. 3) than to the pattern in *X. arizonae* (Fig. 4). The individual large dark dorsal blotches contain 3–28 granular scales versus 4–12 in *X. arizonae* (Fig. 5) and there is a proportionally greater distance from the anterior margin of the eye to the tip of the snout (Fig 6). The new species differs from *X. vigilis* by its larger size, mottled coloration, more than 41 rows of dorsal granular scales and more than 26 lamellae under the fourth toe. It differs from *X. bolsonae*, *X. riversiana*, and *X. henshawi* in having 12 longitudinal rows of ventral scales rather than 14–16 rows. These characters are in addition to substantial differences in allozymes and mitochondrial DNA.

Description of holotype.—Measurements (in mm): Snout-vent length 54; tail length 68 (complete); head length from tip of snout to gular fold 19.8; head width 8.2; fourth toe length, 7.4. Dorsal surface of head: rostral broader than high, followed in order by two nasals in contact medially, two prefrontals, a median prefrontal, two frontals in contact medially, large interparietal separating parietals, and two postparietals in contact medially. Lateral surface of head: nostril bordered by rostral, first supralabial, nasal, and postnasal; anterior loreal, posterior loreal, three loreolabials, four preoculars, four suboculars, five supraoculars, four postoculars, six supralabials, and three pretemporals. Ventral surface of head: mental followed by six pairs of infralabials, four pairs of post mentals, and first pair in contact; gular scales 35 along midline between first pair of post mentals and gular fold. Body surface: dorsal granular scales around body at the 16th transverse row of ventrals 43; ventral scales in 12 longitudinal rows at midbody; transverse rows of ventral scales between gular fold and vent 33; femoral pores on right leg 9, on left leg 11; fourth toe lamellae, 26.

Color pattern in life: dorsal surface of the body with black blotches consisting of 3–28 individual granular scales on a background of cream to tan granular scales; tail coloration similar with black blotches consisting of 1–10 annuli; dorsal surface of head brown with black spots; sides of body similar to dorsal with interspersed white speckling extending to the base of tail; ventral surface of head,

body, and tail cream to tan. Color pattern in preservative is like that in life except the background color of the head is dark and pale gray as opposed to brown.

Variation in paratypes.—The paratypes approximate the holotype in general morphology, pattern, and coloration. The number of femoral pores is 7–11 ($\bar{x}$ = 8.9) per leg. One specimen (MVZ 26415) lacks femoral pores. The number of dorsal granular scales around the body at the 16th transverse row of ventrals is 41–47 ($\bar{x}$ = 44.1). The number of lamellae under the fourth toe is 26–28 ($\bar{x}$ = 27.0.

Habitat and distribution.—The two known localities for *Xantusia bezyi* are in the vicinity of Sunflower at the edge of the Sub-Mogollon Colorado Plateau in an ecotone between the Arizona Upland Subdivision of the Desert Scrub Formation and the Semidesert Grassland of the Grassland Formation (Brown and Lowe, 1980). All individuals were found under pieces of exfoliating rock in granite outcrops (Fig. 1). Suitable habitat is present for about 30 km southwest of Sunflower along Highway 87 toward the Rio Verde. The type locality of *X. arizonae* is 125 km northwest of Sunflower (Fig. 7). Bezy (1967b) reported "granitoform" *Xantusia* from 30 km southeast of Sunflower in the vicinity of Tonto National Monument.

Etymology.—This species is named for Robert L. Bezy in recognition of his lifelong studies on lizards of the family Xantusiidae.

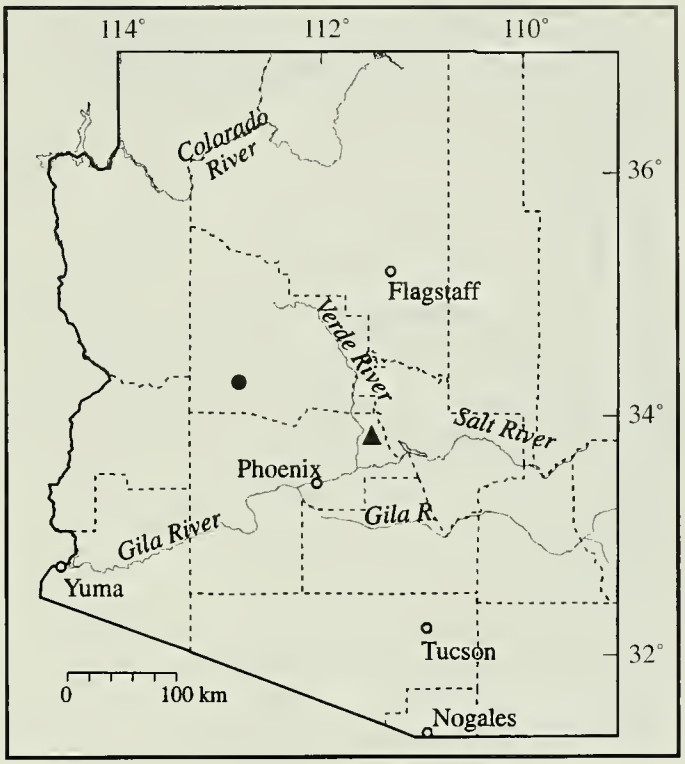

Fig. 7. Map of Arizona showing the type locality for *Xantusia arizonae* (solid circle) and the type locality for *X. bezyi* (triangle).

MOLECULAR VARIATION AMONG *XANTUSIA*

Allozymic variation.—The 28 variable allozymic loci reported by Bezy and Sites (1987) among species of *Xantusia* and *Lepidophyma* were reexamined. Three populations that Bezy and Sites (1987) referred to as *X. vigilis arizonae* belong to three distinct species. The northwestern population (Mojave County) is *X. vigilis* and has only two fixed differences from other populations of *X. vigilis*. The sample of *X. arizonae* from the type locality (Yarnell, Yavapai County) has eight fixed differences from *X. bezyi* (Maricopa County) and 5–7 from populations of *X. vigilis* (Table 1). *Xantusia bezyi* has 9–10 fixed differences from populations of *X. vigilis*. These differences suggest genetic discontinuity between groups of populations here suggested to represent distinct species on the level typically observed between recognized species (for examples in lizards see de Queiroz, 1992; Macey et al., 2000; Sites et al., 1988).

Mitochondrial DNA sequence data.— The mitochondrial gene region of ND1 (subunit one of NADH dehydrogenase), $tRNA^{Ile}$, $tRNA^{Gln}$, $tRNA^{Met}$, ND2, $tRNA^{Trp}$, $tRNA^{Ala}$, $tRNA^{Asn}$, $tRNA^{Cys}$, $tRNA^{Tyr}$, and COI (subunit one of cytochrome *c* oxidase) is reported inTable 2. A single most parsimonious tree (length = 371 steps) produced from phylogenetic analysis of mitochondrial DNA sequences and rooted with *Xantusia henshawi* shows *X. vigilis* and *X. arizonae* to be monophyletic with the exclusion of *X. bezyi* (Fig. 8). The shortest alternative tree showing *X. vigilis* and *X. arizonae* as non-monophyletic is rejected by using the Wilcoxon signed-ranks test with the two-tailed probabilities [Felsenstein, 1985; Templeton, 1983; n = 45; T_s = 345, P < 0.025; alternative tree (*X. henshawi*, ((*X. bezyi*, *X. arizonae*), *X. vigilis*)), L = 386].

Table 1. Pairwise comparisons of Nei (1978) distances (above diagonal) and fixed allozymic differences (below diagonal) among six populations of *Xantusia* reported in Bezy and Sites (1987). In Bezy and Sites (1987), *X. henshawi* is Population 2, *X. bezyi* is Population 3 of *X. v. arizonae*, *X. arizonae* is Population 1 of *X. v. arizonae*. Populations 1 and 2 of *X. vigilis* are numbered the same here as in Bezy and Sites (1987) as *X. v. vigilis*. Population 3 of *X. vigilis* is *X. v. arizonae* Population 2 in Bezy and Sites (1987).

Species	1	2	3	4	5	6
1. *X. henshawi*	—	0.32	0.40	0.32	0.38	0.36
2. *X. bezyi*	11	—	0.29	0.27	0.32	0.36
3. *X. arizonae*	11	8	—	0.19	0.31	0.28
4. *X. vigilis*-1	9	9	5	—	0.10	0.07
5. *X. vigilis*-2	10	10	7	2	—	0.07
6. *X. vigilis*-3	8	9	6	2	2	—

Table. 2. Pairwise comparisons of DNA sequences between species of *Xantusia*. Percentage sequence divergence is shown above the diagonal and the number of base substitutions between sequences is shown below the diagonal.

Species	1	2	3	4
1. *X. henshawi*	—	12.98%	13.91%	13.62%
2. *X. bezyi*	222	—	7.70%	7.59%
3. *X. arizonae*	238	132	—	6.47%
4. *X. vigilis*	233	130	111	—

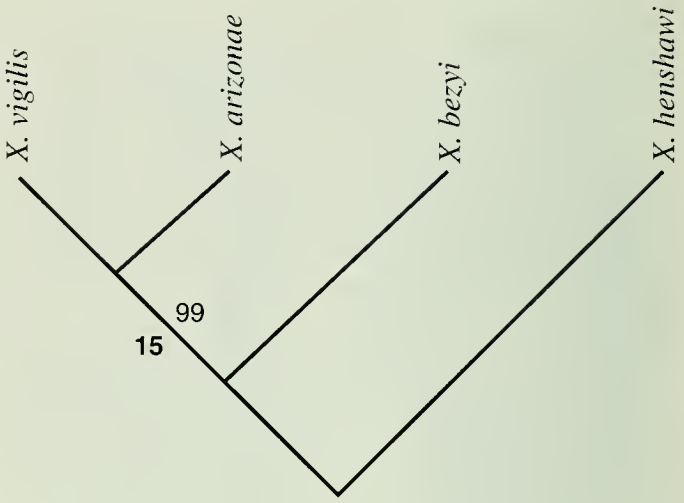

Fig. 8. The single most-parsimonious tree found from an exhaustive search of the 1716 (59 informative) aligned mitochondrial DNA sites showing the root relative to *Xantusia henshawi*. The tree has a length of 371 steps; the bootstrap value is above the branch and the decay index is below the branch in boldface type.The shortest alternative topology requires 15 extra steps (the decay index) and is statistically rejected ($P < 0.025$) applying the conservative two-tailed probability (Felsenstein, 1985) of the Wilcoxon signed ranks test (Templeton, 1983).

The region sequenced has been found to evolve in a clock-like manner among a wide range of vertebrates with a consistent rate of change per lineage per million years [Fish 0.65% (Bermingham et al., 1997); hynobiid salamanders 0.64% (unpublished data of the authors); frogs of the genus *Bufo* 0.69% (Macey et al., 1998b); lizards of the genus *Laudakia* 0.65% (Macey et al., 1998a); lizards of the genus *Teratoscincus* 0.57% (Macey et al., 1999b)].

Pairwise percent sequence divergence between *Xantusia bezyi*, *X. arizonae*, and *X. vigilis* ranges from 6.47% to 7.70%. Using the pairwise rate of 1.3% change per million years, *X. bezyi*, *X. arizonae*, and *X. vigilis* are estimated to have diverged 5–6 million years ago. The amount of sequence divergence among these three species of *Xantusia* is consistent with sequence divergences observed among other species of lizards, salamanders, and frogs (Table 3). Furthermore, we estimate that these three species diverged from *X. henshawi* at least 10 million years ago. This suggests that the genus dates at least to the Miocene.

Table 3. Comparative pairwise sequence divergences between species of amphibians and reptiles. Sequence divergences are calculated for the same segment of mitochondrial DNA spanning from the ND1 gene to the COI gene. Bufonid frogs include only the first half of this segment (from the ND1 gene to the ND2 gene).

Family	Genus	Taxa compared	Pairwise sequence divergences	Reference
Bufonidae	*Bufo*	*B. andrewsi* and *B. gargarizans*	6.0–6.9%	Macey et al. (1998b)
Ranidae	*Rana*	*Rana aurora*, *R. cascadae*, and *R. muscosa*	7.0–8.4%	Macey et al. (2001)
Salamandridae	*Salamandra*	*S. infraimmaculata* and *S. salamandra*	7.4–7.5%	Weisrock et al. (2001)
Agamidae	*Laudakia*	*L. caucasia* and *L. erythrogaster*	4.2–5.3%	Macey et al. (1998a)
Anguidae	*Elgaria*	*E. kingii* to the clade containing *E. multicarinata*, *E. panamintina*, and *E. paucicarinata*	4.8–5.9%	Macey et al. (1999a)
Gekkonidae	*Teratoscincus*	*T. przewalskii* and *L. roborowskii*	6.5%	Macey et al. (1999b)

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