Phylogenetic Relationships and Biogeography of Xantusiid Lizards, Inferred from Mitochondrial DNA Sequences[1]

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Portions of two mitochondrial genes (12S ribosomal RNA and cytochrome *b*) were sequenced in seven species to examine phylogenetic relationships within the lizard family Xantusiidae. Phylogenies derived from these sequences (709 total bp) are concordant and indicate that the Cuban species *Cricosaura typica* is the sister group to all other xantusiids. The Middle American genus *Lepidophyma* is the closest relative of *Xantusia,* and *X. riversiana* (California Islands) the closest relative of *X. vigilis* (mainland). These findings are not in agreement either with the results of a recent morphological analysis that united *Cricosaura* and *Lepidophyma* as closest relatives or with past studies that have recognized *X. riversiana* as a separate genus. Levels of sequence divergence, as well as the age and affinities of some mainland fossil taxa, suggest that the origin of *Cricosaura* was associated with the tectonic evolution of the Greater Antilles in the late Cretaceous. These results further demonstrate that significant resolution of phylogenies can be obtained with relatively short DNA sequences and that these mitochondrial genes are concordant in their estimation of phylogeny.

Introduction

The ability to amplify and sequence DNA rapidly (Mullis et al. 1986; Saiki et al. 1988) and the existence of "universal" oligonucleotide (primer) sequences with utility across a broad taxonomic range (Kocher et al. 1989) are certain to have a major impact on systematics. Although universal primers are by no means limited to mitochondrial genes, most of the initial studies have utilized primers for the mitochondrial 12S ribosomal RNA (rRNA), cytochrome *b* genes, and the noncoding control region (Thomas et al. 1989, 1990; Meyer et al. 1990; Meyer and Wilson 1990; Smith and Patton 1991). They have illustrated how DNA sequence data can be generated rapidly from living, preserved, and fossil organisms to address a variety of systematic questions. The same approach is used in the present study to investigate the relationships and biogeography of the enigmatic lizard family Xantusiidae.

The Xantusiidae has been of special interest to reptilian systematics and biogeography because of both the uncertainty of its phylogenetic position among lizard families and its peculiar geographic distribution (fig. 1). Xantusiid lizards occur in three disjunct regions: western North America (*Xantusia,* four species), Middle America (*Lepidophyma,* 14 species), and Cuba (*Cricosaura,* one species). The Cuban species (*C. typica*) is of particular interest, as it represents a biogeographic anomaly. It is the

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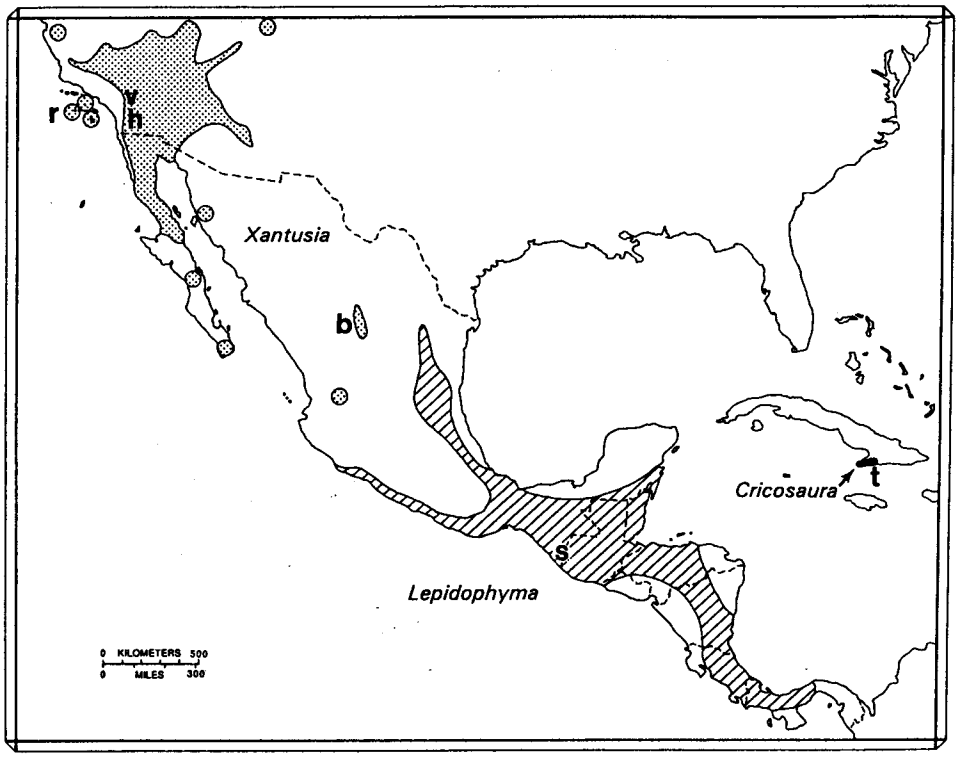

FIG. 1.—Distributions of xantusiid lizards. Localities of all three extant taxa are indicated by letters: b = *Xantusia bolsonae;* h = *X. henshawi;* r = *X. riversiana;* v = *X. vigilis;* s = *Lepidophyma smithii;* and t = *Cricosaura typica.*

only xantusiid lizard in the West Indies, yet it occurs in a remote and isolated area of eastern Cuba, far removed from the nearest mainland representatives of the family. No xantusiids occur in western Cuba, the Cayman Islands, or Jamaica, areas that are closer to the mainland.

The phylogenetic relationships among xantusiids have been examined using evidence from chromosomes (Bezy 1972), allozymes (Bezy and Sites 1987), and morphology (Peterson and Bezy 1985; Crother et al. 1986; Bezy and Peterson 1988). However, the chromosome and allozyme analyses were hindered by the inability to obtain live specimens of *C. typica,* and the morphological analyses were impeded by the small number of characters that were informative under the conditions of parsimony. Here we present an analysis of mitochondrial DNA sequences that challenges recent hypotheses of xantusiid phylogeny based on nonmolecular data, provides the first robust estimate of intergeneric relationships in this family, and has implications for current models of Caribbean biogeography.

Methods

DNA was extracted from small amounts (<50 mg) of liver or intestine from the following species of xantusiid lizards: *Cricosaura typica* (National Museum of Natural History, USNM, 306539; Cuba: Santiago de Cuba: 2.8 km N Uvero), *Lepidophyma smithii* (Natural History Museum of Los Angeles County, LACM, 136359; Mexico: Chiapas: 2.5 mi NE Acacoyagua), *Xantusia bolsonae* (LACM 138478; Mexico: Dur-

ango: 3.2 mi SW Chocolate), *X. henshawi* (LACM 136789; California: Riverside Co.: 4.7 mi SE Banning), *X. riversiana* (LACM 125513; California: Ventura Co.: San Nicolas Island), and *X. vigilis* (LACM 136813; California: San Bernardino Co.: Hesperia). The teiid lizard *Ameiva auberi* (USNM 306540; Cuba: Guantánamo Prov.: 8.9 km SW Hatibonico) was used to root the phylogenetic trees. In the absence of a current consensus regarding the sister group of the Xantusiidae (Estes et al. 1988; Presch 1988; Schwenk 1988), we use a member of the Teiidae to root the trees, as it is clearly an outgroup to the Xantusiidae and is a member of what may be one of the closest lineages (Estes et al. 1988).

The tissue was minced and placed in 500 μl of extraction buffer [100 mM Tris HCl (pH 8.0), 10 mM ethylenediaminetetraacetate (pH 8.0), 100 mM NaCl, 0.1% SDS, 50 mM dithiothreitol, and 0.5 μg proteinase K/ml; Kocher et al. 1989) for 2 h at 37°C, with slight agitation. Purification was by phenol (twice) and chloroform (once) extractions followed by ethanol precipitation. The DNA precipitate was spin-dried under vacuum and was resuspended in 10 μl sterile distilled H_2O. One microliter of a 1:1,000 dilution of the extracted DNA was used as a template for the double-stranded polymerase-chain-reaction (PCR) amplification, which was performed in 25 μl of a solution containing 67 mM Tris (pH 8.8), 6.7 mM $MgSO_4$, 16.6 mM $(NH_4)_2SO_4$, 10 mM 2-mercaptoethanol, each dNTP at 0.1 mM, each primer at 1 μm, and 0.5 units of AmpliTaq (*Thermus aquaticus* DNA polymerase; Perkin Elmer—Cetus) and capped with 1 drop of mineral oil. A negative-control tube (no template) was included with each run. After 30 cycles (93°C for 1 min, 50°C for 1 min, 72°C for 2.5 min), 10 μl of the amplified reaction mix was purified in a 2% low-melting-temperature agarose (NuSieve; FMC) gel (0.89 M Tris, 0.89 M boric acid, and 0.002 M ethylenediaminetetraacetate); a single core was removed from each band (stained with ethidium bromide) with a sterile pasteur pipette, and the band core was melted in 1 ml of sterile distilled H_2O at 93°C for 5 min. A second PCR amplification with one primer reduced to $^1/_{100}$ of its original concentration (Gyllensten and Erlich 1988) was used to generate single-stranded DNA by using 1 μl of the diluted band melt as the template (30–35 cycles; 93°C/60°C/72°C; 50-μl vol.). The single-stranded product was purified with three passes in a 100,000-MW filter (Millipore), and the final volume was adjusted, by centrifugation, to 7 μl for dideoxy sequencing (Sanger et al. 1977).

Two segments of the mitochondrial genome were sequenced: a 307-bp region of the cytochrome *b* gene (primers 5′-AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA-3′ and 5′-AAACTGCAGCCCCTCAGAATGATATTTGTCCTCA-3′) and an ~400-bp region of the 12S rRNA gene (primers 5′-AAAAAGCTTCAAACTGGGATTAGATACCCCACTAT-3′ and 5′-TGACTGCAGAGGGTGACGGGCGGTGTGT-3′) (Kocher et al. 1989). In each case, both complementary strands were sequenced using the two PCR primers as sequencing primers in separate reactions. For each reaction, the limiting primer in the second (single-stranded) amplification was used as the sequencing primer. A modified form of T7 DNA polymerase was used in the Sequenase (United States Biochemical) protocol, with the following changes: the annealing mix was heated at 90°C (for 6 min), cooled at room temperature (for 1 min), combined with label reaction mix (4°C), and then added to termination mix and incubated at 37°C (for 3 min). Sequenced products were separated on two (3 and 7 hr) 6% polyacrylamide wedge gels.

Sequence data were read from autoradiograms by using a digitizing program (S. W. Schaeffer, Penn State University), and alignments were done by eye by using the multisequence editing program ESEE (Cabot and Beckenbach 1989). Because the

ratio of the number of characters to the number of taxa is large, a phenetic analysis (Sokal 1985) was not used. Nucleotide sequence and length variation were analyzed by the maximum-parsimony (MP) method (Phylogenetic Analysis Using Parsimony, version 3.0; D. L. Swofford, Illinois Natural History Survey, Urbana). Every length difference of one or more bases was scored as a single event with two states (insertion or deletion); sequences within the inserted region then were analyzed normally, with the deleted bases scored as ambiguities (i.e., missing information). This was done so that informative sequence variation within an insertion could be utilized. Each consistency index (CI) is based on sites that are informative under the conditions of parsimony (i.e., those sites with at least two bases, each occurring in more than one taxon). A distance matrix of sequence divergence (Jukes and Cantor 1969) among the taxa was analyzed by the neighbor-joining (NJ) method (Saitou and Nei 1987, version 2.0; Studier and Keppler 1988). The statistical significance of the groups in both analyses was evaluated by the bootstrap method (Felsenstein 1985), with 1,000 iterations. The programs PSFIND and NJBOOT (T. S. Whittam, Penn State University) were used with the NJ analyses to find polymorphic sites and to obtain bootstrap confidence limits, respectively.

Results

For the 12S rRNA segment (fig. 2), there are 402 total aligned sites, 208 of which are variable (94 are informative under the conditions of parsimony). For the cytochrome *b* segment (fig. 3), there are 307 total aligned sites, 157 of which are variable (74 are informative under the conditions of parsimony). In cytochrome *b*, 43/99 amino acid positions are variable, nine of which are different only in the outgroup (*Ameiva*). The number of transitions and transversions for all pairwise comparisons are in table 1, and, for both genes, percent transitions is plotted against percent sequence divergence, in figure 4.

The region of cytochrome *b* sequenced lies almost entirely between the two highly conserved domains believed to be important in the function of the protein (Howell 1989), and therefore little can be gleaned from the distribution of variable amino acid positions. However, the two histidine positions involved in heme ligation are unvaried (fig. 3), as predicted by the structural model (Howell and Gilbert 1988). The total number of variable sites is sufficient to result in distances with relatively low error estimates (Martin et al. 1990).

The MP and NJ analyses of the 12S rRNA data produced identical topologies (fig. 5, *top*). The CI for the 12S rRNA MP tree is 0.85. The MP (CI 0.77) and NJ analyses of the cytochrome *b* data also produced identical topologies (fig. 5, *middle*), although (*a*) the confidence limits were lower and (*b*) the position of *Xantusia bolsonae* differs from its position in the 12S rRNA trees. In contrast to the 12S rRNA analyses, the highest confidence limits in the cytochrome *b* analyses were associated with close relationships (*X. riversiana* and *X. vigilis*). The combined analysis (12S rRNA and cytochrome *b*) yielded MP (CI 0.81) and NJ trees that have highly significant confidence limits on three of the four nodes (fig. 5, *bottom*) and that differ only in the position of *X. bolsonae.*

An ongoing study of amniote phylogeny (S. B. Hedges and L. R. Maxson, unpublished data) provided the opportunity to examine the effect that outgroup had on xantusiid relationships at 12S rRNA. Sequences from two other lizard families suggested as possible sister groups or members of sister groups to the Xantusiidae (Presch 1988; Schwenk 1988), the Gekkonidae (*Gekko*) and Scincidae (*Eumeces*), were used as

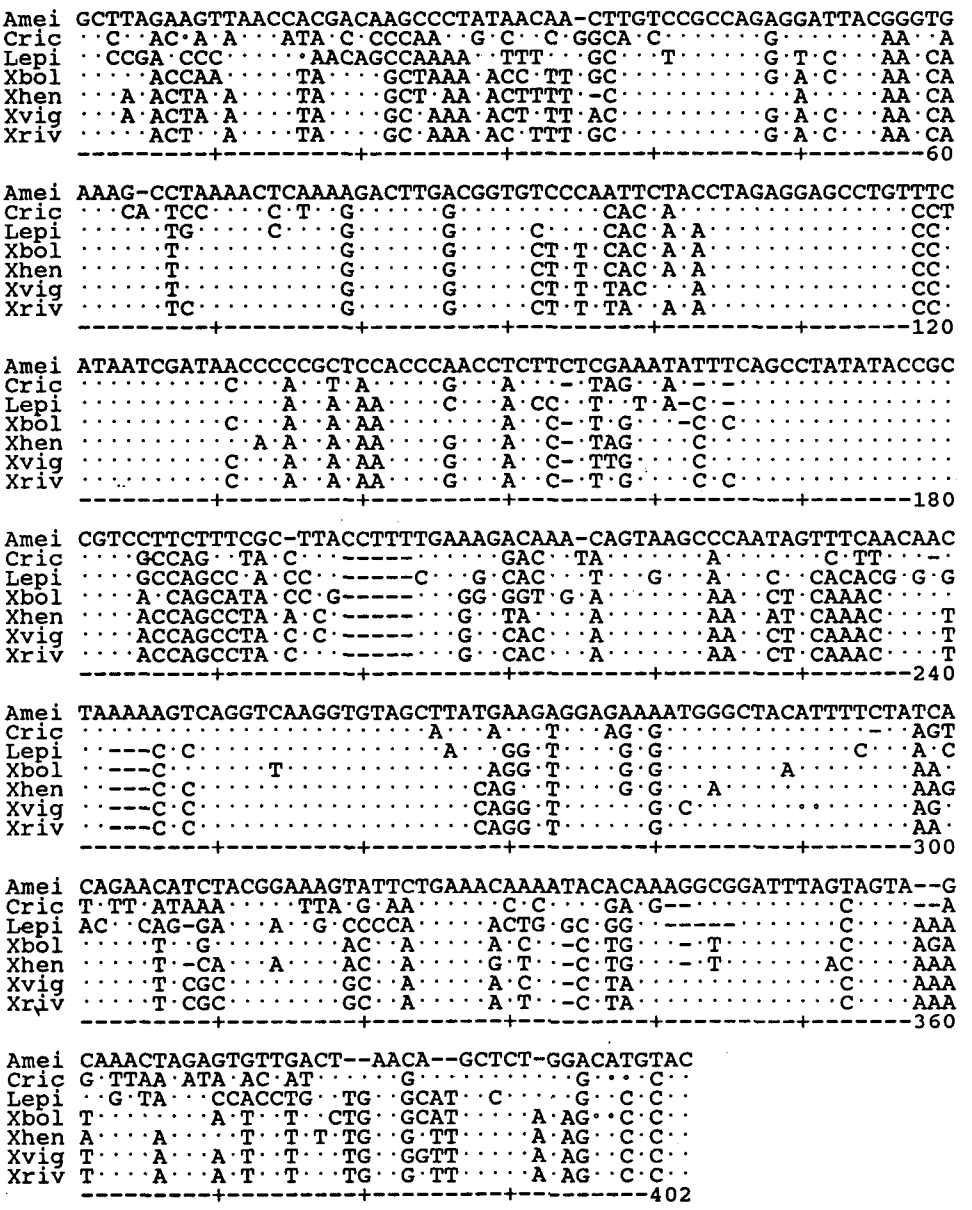

FIG. 2.—DNA sequences of portion of 12S rRNA gene (corresponding to sites 1092–1477 in human; Anderson et al. 1981) in seven taxa of lizards. A solid dot (·) denotes identity with the first sequence; a dash (-) denotes a gap; and a small circle (○) denotes an ambiguity.

outgroups in place of the Teiidae, resulting in relationships that were identical to those in fig. 5 (*top*) and that had statistically significant nodes.

Discussion

Molecular Evolution

The pattern of nucleotide substitution among the cytochrome *b* sequences is similar to that observed in previous studies: synonymous differences are more numerous

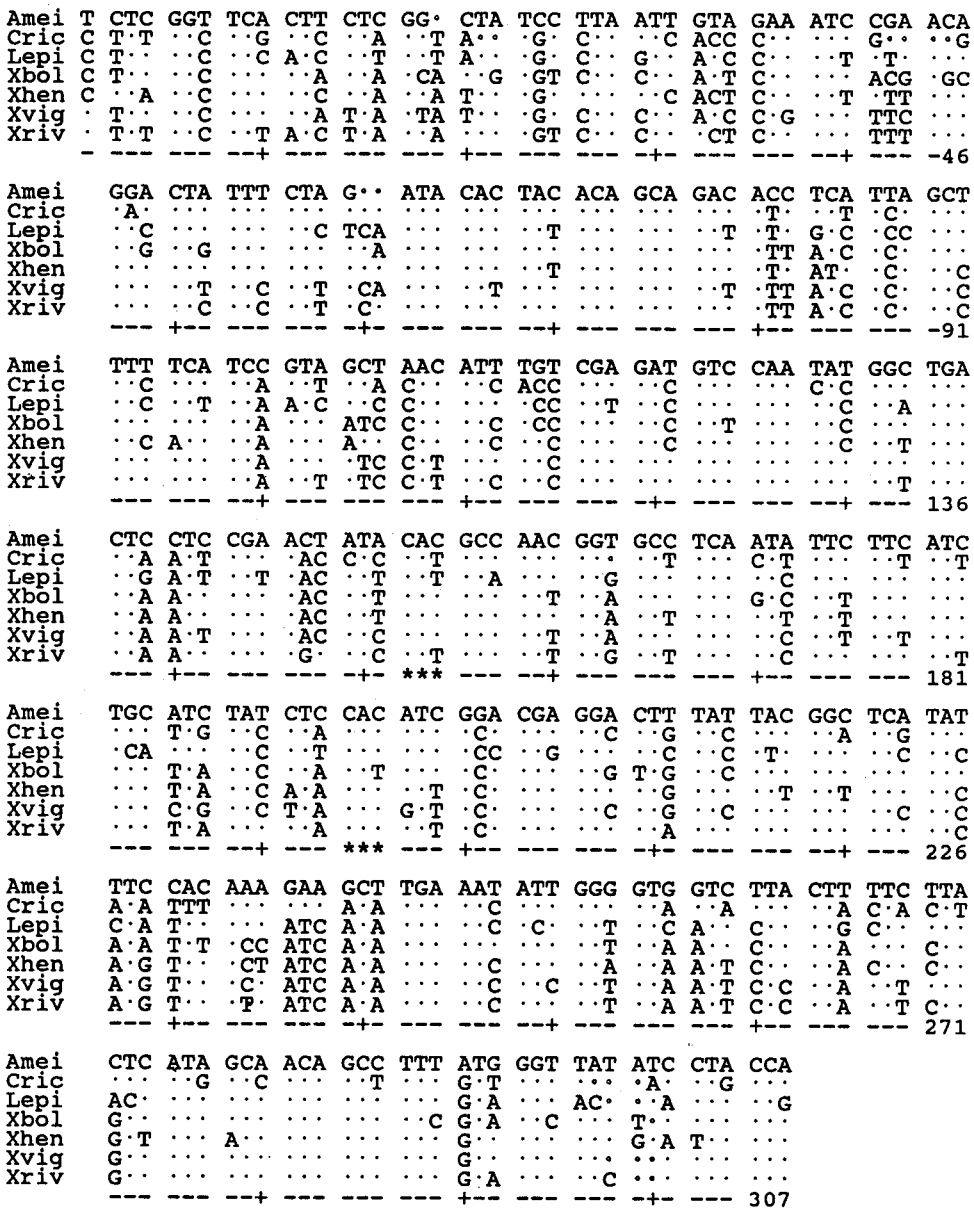

FIG. 3.—DNA sequences of portion of cytochrome *b* gene (corresponding to sites 14842–15148 in human) in seven taxa of lizards. Symbols are as in fig. 2. Asterisks (*) denote the two unvaried histidine positions involved in heme ligation (Howell and Gilbert 1988).

than nonsynonymous differences (Brown et al. 1982; Brown 1985; Wilson et al. 1985; Meyer et al. 1990; Meyer and Wilson 1990; Smith and Patton 1991). In both 12SrRNA and cytochrome b, transitions exceed transversions at low levels of sequence divergence but are in relatively equal frequencies at high levels of divergence (fig. 5). This finding also agrees with previous studies and reflects the initially high transition bias of mitochondrial DNA, which gradually decreases over time as transversions accumulate (Brown et al. 1982; Brown 1985; Hixson and Brown 1986; DeSalle et al. 1987). The

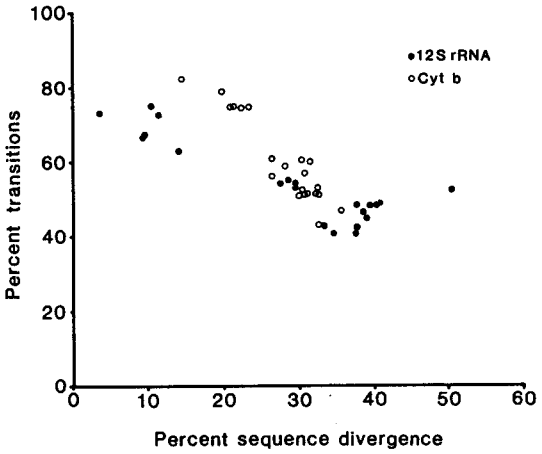

FIG. 4.—% Transitions vs. % sequence divergence, in seven taxa of lizards

presence of this transition bias in sequence comparisons has been used to assess the adequacy of those sequences for phylogenetic analysis. Comparisons showing no abundance of transitions suggest that a plateau has been reached (usually 40%–45% transitions) whereby multiple substitutions are occurring at the same site (multiple hits), thus limiting their usefulness in estimating phylogeny (Brown et al. 1982; Thomas et al. 1989).

In the present study, a transition bias is evident in most of the ingroup comparisons (table 1 and fig. 4), suggesting that these sequence data, in general, have not been adversely affected by multiple hits. However, we refrain from making any divergence-time estimate based on percent transitions and percent divergence, for two reasons. First, the mechanisms responsible for the transition bias appear to be different in RNA genes (rRNA and tRNA) versus protein-coding genes (Brown 1985; Hedges et al. 1990). Second, the substitution rate varies among nonsynonymous sites, within and among protein-coding genes, between the rRNA genes, and between regions (stems vs. loops) of those genes (Mindell and Honeycutt 1990). These factors combined would indicate that there is no reason to expect a universal transition or sequence-divergence curve in mitochondrial DNA, except perhaps with regard to synonymous sites (Ochman and Wilson 1987). Synonymous sites become saturated very quickly (Brown et al. 1982), but then the rate at which nonsynonymous sites become saturated will vary depending on the gene and region within the gene, because of different functional constraints.

Often some highly variable regions within a gene (especially rRNA) that are alignable among closely related populations become unalignable—and therefore must be omitted from the analysis—when more divergent populations or taxa are compared (e.g., see Hedges et al. 1990; Meyer and Wilson 1990). In such cases, it is not valid to use the same molecular-clock calibration, because that calibration has changed with the deletion of those variable regions, even though the total segment sequenced is identical. Similarly, functionally constrained regions of low variability within cytochrome *b* (Howell 1989) indicate that clock calibrations for particular segments of this gene (such as the one sequenced in the present study) are applicable only to those segments. Finally, the substitution rate varies to some degree among different taxonomic groups (Mindell and Honeycutt 1990). Despite all of these caveats, the average

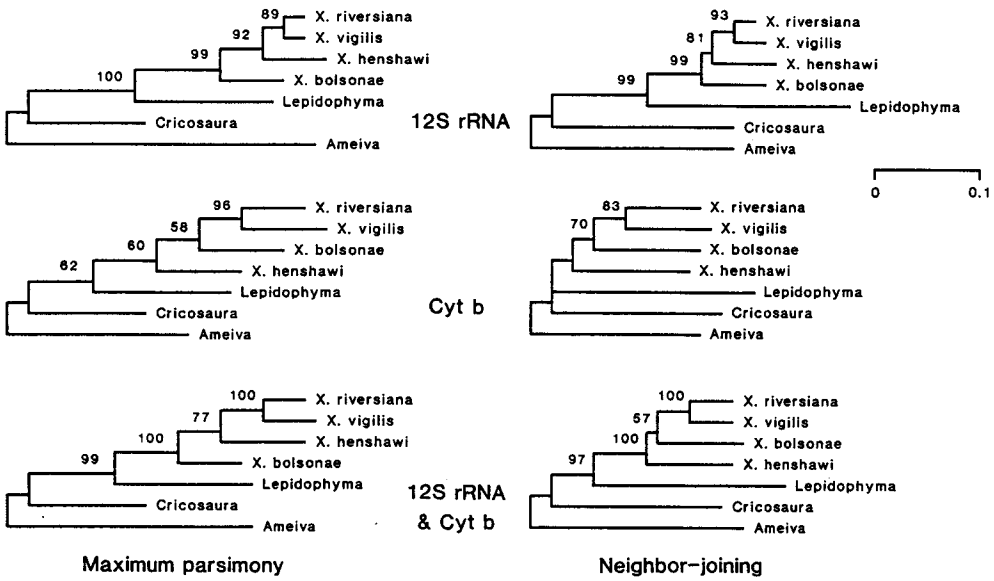

FIG. 5.—Relationships among six species of lizard family Xantusiidae, obtained by maximum-parsimony and neighbor-joining methods. *Ameiva auberi* (Teiidae) was used to root the trees. Numbers on trees indicate the percentage of bootstrapped trees supporting each node.

sequence divergence between *Cricosaura* and other xantusiid lizards—for both cytochrome *b* (28.8%) and 12SrRNA (36.5%)—is comparable to or greater than that observed between different orders of mammals (Primates, Rodentia, and Artiodactyla) believed to have diverged in the late Cretaceous: for regions sequenced in the present study, the average divergence between *Homo sapiens* (Anderson et al. 1981), *Mus musculus* (Bibb et al. 1981), and *Bos taurus* (Anderson et al. 1982) is 28.9% for cytochrome *b* and 21.2% for 12S rRNA. When only a conserved 12S rRNA fragment that corresponds to sites 1135–1275 in the human sequence (Anderson et al. 1981) and appears to show a relatively constant rate of change (Mindell and Honeycutt 1990) is considered, the average percent sequence divergence (16.4%) between *Cricosaura* and other xantusiids implies an unrealistically early divergence (200–300 Mya), although a large variance is to be expected from such a small total number (140–150) of sites.

The effect that rRNA secondary structure has on phylogenetic inference is not well understood. It has been suggested that nucleotide positions in stem regions are under strong selection to maintain basepairing and that therefore any substitutions causing a mismatch will lead to a compensatory substitution reestablishing the basepairing (Brown 1985; Hixson and Brown 1986). Although covariation of paired differences in some 5S rRNAs suggests that compensatory changes do occur (Wheeler and Honeycutt 1988), it is unclear what proportion are involved and how this can be accounted for in a phylogenetic analysis. Wheeler and Honeycutt (1988) recommended either weighting paired sites as one-half or deleting them entirely from the analysis. The first recommendation implies that all changes in stem regions result in compensatory substitutions, something that has not been demonstrated. Many stem regions contain bulges of one or more mismatches that increase or decrease in size over time (Hassouna et al. 1984; Michel and Westhof 1990), indicating that a signif-

Table 1
Number of Transitions (above diagonal) and Number Transversions (below diagonal)

	12S rRNA							*Cytochrome b*						
	Am	Cr	Le	Xb	Xh	Xv	Xr	Am	Cr	Le	Xb	Xh	Xv	Xr
Am		49	70	55	55	55	53		40	41	42	44	41	39
Cr	61		48	44	42	40	40	38		34	40	37	44	41
Le	63	55		48	48	48	45	45	44		40	38	40	47
Xb	57	57	38		30	29	28	38	26	37		44	42	42
Xh	56	57	42	18		22	23	33	29	37	15		45	42
Xv	57	55	39	11	11		11	38	29	36	11	15		33
Xr	55	51	37	9	11	4		37	28	31	14	14	7	

NOTE.—Am = *Ameiva;* Cr = *Cricosaura;* Le = *Lepidophyma;* Xb = *Xantusia bolsonae;* Xv = *X. vigilis;* and Xr = *X. riversiana.*

icant proportion of mismatched differences are tolerated. The second recommendation—i.e., to delete paired sites—was based on Wheeler and Honeycutt's finding, in an analysis of some 5.85 rRNA data, that such sites resulted in a "misleading" phylogeny. However, their "known" phylogeny was one based on morphology (possibly incorrect), the number of sites involved was very small, no statistics (e.g., see Felsenstein 1985) were used to assess the significance of the groups, and no explanation was given as to why paired sites should provide misleading information. Moreover, two subsequent studies using larger data sets (Smith 1989; Hedges et al. 1990) have not supported that finding. Other factors to be considered are that minor sequence differences can yield different secondary structures, the proximity of complementary regions during rRNA synthesis may influence folding patterns (Mindell and Honeycutt 1990), and sites that are basepaired in some taxa may not be paired in other taxa. The last factor will necessarily complicate any character(=site)-weighting scheme.

Until now, only secondary structure has been considered, but recent studies of group I catalytic introns have demonstrated that there is significant covariation between distant sites related only by tertiary structure (Michel and Westhof 1990) and that such higher-order folding can be affected by ionic composition (Celander and Cech 1991). The complex tertiary structures of some 5S rRNAs recently have been modeled at atomic resolution (Westhof et al. 1989), but no such models exist for the larger rRNA molecules. Although single-stranded (loop) regions tend to be more variable, some have conserved sites known to be involved in tertiary interactions and, in other cases, in protein binding (Westhof et al. 1989). Atomic and molecular interactions within the ribosome place constraints on the kinds and rates of rRNA nucleotide substitution, but our present knowledge of these constraints is insufficient to make adjustments in methods of phylogenetic analysis. Therefore we believe that a scheme using equal weighting is currently the best approach.

Phylogeny

DNA sequences from these two mitochondrial genes are highly concordant in their conveyance of evolutionary relationships (fig. 5). The slightly lower levels of support for nodes in the cytochrome *b* trees are likely the result of saturation at many synonymous sites, increasing the "noise" level (note, in figs. 2 and 3, sites with three or four different bases present). For this reason, the phylogenetic information present

in the cytochrome *b* data set is more useful for close relationships (e.g., *Xantusia vigilis* and *X. riversiana*), whereas the 12S rRNA data set is more informative for the older branches of xantusiid phylogeny (*Cricosaura* and *Lepidophyma*). This is reflected in the confidence limits on the 12S rRNA and cytochrome *b* trees (fig. 5). Combined, the differential resolution of the two data sets complement one another and result in a highly resolved phylogeny (fig. 5, *bottom*).

These results offer a different view of xantusiid phylogeny and biogeography than has been obtained from recent analyses of morphology. *Cricosaura typica* is shown here to be the oldest separate lineage (first to diverge), whereas a recent morphological analysis by Crother et al. (1986) united it with *Lepidophyma.* In that study, however, only two informative characters supported a *Cricosaura* + *Lepidophyma* grouping, and the large amount of morphological change along those two lineages (*Cricosaura* and *Lepidophyma*) resembles a model (Felsenstein 1978, 1988) whereby parsimony methods fail because of the "attraction" (convergence) of long branch lengths. Moreover, a reanalysis of Crother et al.'s data (PAUP 3.0, CI 0.69) results in no statistically significant groups, which is not surprising when one considers that at least three supporting characters are needed for statistical significance (Felsenstein 1985). In the present study, 31 sites support the *Lepidophyma+Xantusia* grouping by the parsimony criterion (with no homoplasy), whereas only 13 sites support a *Lepidophyma+Cricosaura* grouping and only four sites support a *Xantusia+Cricosaura* grouping. Variation in scale-surface microstructure has been useful in defining both the genus *Lepidophyma* and groups within that genus but has not provided information on intergeneric relationships (Peterson and Bezy 1985; Bezy and Peterson 1988). Our findings for *Cricosaura* are in agreement both with earlier phenetic interpretations of the morphological data (Savage 1963; Schatzinger 1980) and with recent chromosomal evidence. *Cricosaura typica* has a karyotype ($2N = 24$) consisting of 12 macrochromosomes (Hass and Hedges, accepted), which is considered to be primitive compared with the 16–18 macrochromosomes found in *Lepidophyma* and *Xantusia* (Bezy 1972).

The DNA sequence data also provide a new view of phylogenetic relationships within the genus *Xantusia.* They indicate that *X. riversiana* is the sister species of *X. vigilis,* whereas the available interpretations of morphological data place it as the sister species of all other *Xantusia* (Savage 1963; Schatzinger 1980; Crother et al. 1986). The position of *X. riversiana* in the sequence phylogeny (fig. 5) corresponds with that in a phenetic analysis of allozyme data (Bezy and Sites 1987, fig. 1)—but it does not correspond with a parsimony analysis of the same allozyme data, which places it as the sister species of *X. henshawi* (Bezy and Sites 1987, fig. 3). It should be noted that the *X. riversiana–X. vigilis* node in the present study is supported by high confidence limits in all trees. Both the sequence and the allozyme data indicate that *X. riversiana* was derived from within *Xantusia* and should not be considered as a separate genus (*Klauberina;* Savage 1957, 1963).

The sequence data also agree with the allozyme data in indicating that *X. bolsonae* and *X. henshawi* are not closest relatives and thus should not be considered conspecific (Bezy and Sites 1987). However, the allozyme and sequence phylogenies differ in detail: the sequence data do not place *X. bolsonae* as the sister group of any other *Xantusia* species, whereas the allozyme data place it as the sister species of the sympatric population of *X. vigilis.* As this population of *X. vigilis* was not included in the present study, and as the position of *X. bolsonae* differed in some analyses, sequence data from additional individuals and populations of *Xantusia* will be required to fully resolve relationships within the genus.

Biogeography

If the phylogenetic relationships found here are correct, they require a reevaluation of the biogeographic history of xantusiid lizards. Members of the fossil genus *Paleoxantusia* are known to have existed at least as early as the Middle Paleocene, ~60 Ma (Estes 1976). Although the phylogenetic relationships of the members of *Paleoxantusia* remain poorly resolved, the latter apparently share derived features with *Xantusia* and *Lepidophyma* (rather than with *Cricosaura*) and are considered to be members of the Xantusiinae (Savage 1963; Schatzinger 1980). The appearance of *P. fera* in the Paleocene suggests that the divergence between *C. typica* and the other xantusiids may date at least from the late Cretaceous, an inference which is not refuted by the level of sequence divergence between *Cricosaura* and other xantusiids, as noted above.

Recent plate-tectonic reconstructions of the Caribbean region place the Greater Antilles (including Cuba) in an island arc connecting North America and South America during the late Cretaceous (Burke 1988; Ross and Scotese 1988). The breakup of this island arc may have isolated *Cricosaura* on Cuba from the remaining xantusiid stock on the mainland. Although *Cricosaura* may have occurred on other Antillean islands, the West Indian Tertiary fossil record for terrestrial vertebrates is poor, and there are no xantusiids represented (Williams 1989). If *C. typica* is a proto-Antillean relict, then it is one of the few living examples. Recent molecular evidence indicates that, with the possible exception of some eleutherodactyline frogs (Hedges 1989), most of the extant West Indian terrestrial vertebrate groups arose by dispersal from the mainland rather than by vicariance (Hedges et al., submitted).

The sequence data suggest that, after the origin of *C. typica* in the late Cretaceous, the mainland xantusiids diverged into a *Xantusia* clade and a *Lepidophyma* clade. This probably occurred sometime prior to the late-Eocene appearance of two species (Schatzinger 1980) of "*Paleoxantusia*" that share derived features with *Lepidophyma* (*P. kyrentos*) and *Xantusia* (*P. allisoni;* Estes 1983; Gauthier, in Sullivan 1982). Although the present distributions of *Xantusia* and *Lepidophyma* (fig. 1) suggest a vicariant event, the Eocene coexistence of these two lineages in western North America (Schatzinger 1980) indicates that significant changes in distribution have occurred. Details of the historical events within *Xantusia* and *Lepidophyma* are more difficult to ascertain, because of both the scant fossil record and the morphological convergence suggested by the molecular data. On the basis of morphology, the Neogene fossil species *X. downsi* has been interpreted as being the sister group of *X. vigilis–X. henshawi* (Norell 1989), but the molecular data indicate that these two species do not constitute a monophyletic group exclusive of *X. riversiana.*

Sequence Availability

The sequences shown in figure 2 have been deposited in GenBank under accession numbers M65110–M65116. The sequences shown in figure 3 have been deposited in GenBank under accession numbers M65117–M65123.

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