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Phylogenetic relationships within the lizard clade Xantusiidae: Using trees and divergence times to address evolutionary questions at multiple levels

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ABSTRACT

Xantusiidae (night lizards) is a clade of small-bodied, cryptic lizards endemic to the New World. The clade is characterized by several features that would benefit from interpretation in a phylogenetic context, including: (1) monophyletic status of extant taxa *Cricosaura*, *Lepidophyma*, and *Xantusia*; (2) a species endemic to Cuba (*Cricosaura typica*) of disputed age; (3) origins of the parthenogenetic species of *Lepidophyma*; (4) pronounced micro-habitat differences accompanied by distinct morphologies in both *Xantusia* and *Lepidophyma*; and (5) placement of *Xantusia riversiana*, ~~the only~~ vertebrate species endemic to the California Channel Islands, which is highly divergent from its mainland relatives. This study incorporates extensive new character data from multiple gene regions to investigate the phylogeny of Xantusiidae using the most comprehensive taxonomic sampling available to date. Parsimony and partitioned Bayesian analyses of more than 7 kb of mitochondrial and nuclear sequence data from 11 loci all confirm that Xantusiidae is monophyletic, and comprises three well-supported clades: *Cricosaura*, *Xantusia*, and *Lepidophyma*. The Cuban endemic *Cricosaura typica* is well supported as the sister to all other xantusiids. Estimates of divergence time indicate that *Cricosaura* diverged from the (*Lepidophyma* + *Xantusia*) clade ~81 million years ago (Ma), a time frame consistent with the separation of the Antilles from North America. Our results also confirm and extend an earlier study suggesting that parthenogenesis has arisen at least twice within *Lepidophyma* without hybridization, that rock-crevice ecomorphs evolved numerous times (>9) within *Xantusia* and *Lepidophyma*, and that the large-bodied Channel Island endemic *X. riversiana* is a distinct, early lineage that may form the sister group to the small-bodied congeners of the mainland.

1. Introduction

Crown Xantusiidae is a clade (traditionally ranked as a family) of primarily reclusive lizards comprising three genera endemic to the New World: *Cricosaura* (1 species confined to southeastern Cuba; Savage, 1964; Crother, 1988), *Lepidophyma* (~19 species in Middle America; Bezy and Camarillo, 2002; Canseco-Márquez et al., 2008; García-Vázquez et al., 2010), and *Xantusia* (~14 species in the southwestern U.S. and northwestern Mexico; Sinclair et al., 2004; Leavitt et al., 2007; Bezy et al., 2008) (Fig. 1).

Despite several prior studies investigating relationships of the night lizards, important aspects of their phylogeny remain unresolved. Early work on this group was based on osteology and scalation (Savage, 1955, 1963; Crother et al., 1986) and supported a (*Xantusia* + *Klauberina* [=*X. riversiana*]) (*Lepidophyma* + *Cricosaura*) topology. These were followed by analyses of mtDNA regions (e.g. 12S, 16S, and cytochrome *b*) supporting (*Cricosaura* (*Lepidophyma*, *Xantusia*)), with the formerly recognized monospecific genus *Klauberina* (*X. riversiana*) embedded within *Xantusia* (Hedges et al., 1991; Hedges and Bezy, 1993; Vicario et al., 2003; Sinclair et al., 2004) though the morphological study of Conrad (2008) supported a topology with the positions of *Lepidophyma* and *Cricosaura* reversed. Recently, Gauthier et al. (2012) analyzed a large phenotypic data set and also found weak support for (*Cricosaura* + *X. vigilis*),

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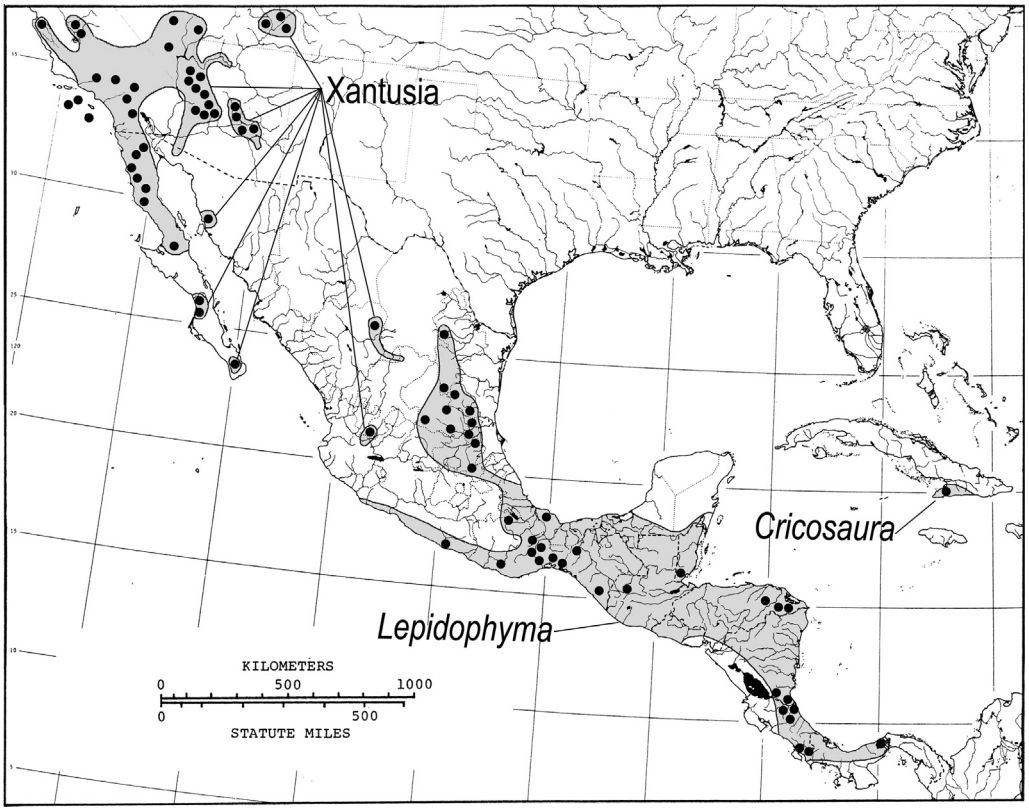

Fig. 1. Map of the southwestern United States, Mexico, Central America, and the western Caribbean showing the geographic distribution of extant Xantusiidae and sampling localities (dots).

but considered the association of these species to be strongly influenced by their small body size. Importantly, all prior studies investigating relationships within the night lizards were based on limited marker, taxon and population sampling within *Lepidophyma*. Limited taxon sampling can strongly bias phylogenetic conclusions at both intra- and interspecific levels (Gauthier et al., 1988a; Donoghue, 1989; Lecointre et al., 1993; Hedin 1997; Poe 1998), and may also confound the ability of phylogenetic algorithms to accurately reconstruct ancestral character states (Pollock et al., 2002; Hillis et al., 2003). These problems were compounded in previous studies by a lack of a clearly resolved outgroup for Xantusiidae, but this has since been resolved (Gauthier et al. 2012; Wiens et al. 2012).

Xantusiidae is characterized by several interesting evolutionary features that justify additional detailed phylogenetic study. For example, the Cuban endemic *Cricosaura typica* is the only xantusiid found in the West Indies. It has been suggested that this enigmatic species is one of the few autochthonous Caribbean vertebrate species that may represent a lineage whose divergence from its mainland relatives predates the asteroid impact at the KT boundary (65 Ma; Hedges et al., 1991). More recent studies estimating the divergence time for this lineage include estimates that both postdate (56 Ma; Vicario et al., 2003) and pre-date (76 Ma; Roca et al., 2004; Hedges, 2006) the KT boundary, so the issue remains unresolved.

There also are unresolved questions of broad evolutionary significance within *Lepidophyma* and *Xantusia*. In the former, several populations of *L. flavimaculatum* and all known populations of *L. reticulatum* are unisexual (and presumably parthenogenetic). Previous studies of unisexual *L. flavimaculatum* have failed to confirm the patterns of fixed heterozygosity (for Mendelian markers diagnostic of the sexually reproducing species) expected from a model of a hybrid origin (Bezy and Sites, 1987). Sinclair et al. (2010) recently showed that the most parsimonious phylogenetic interpretation supported two independent origins of unisexuality in *Lepidophyma*, one in the ancestor of all *L. reticulatum*, and later a second time in the ancestor of some populations of *L. flavimaculatum*. Further, neither of these met expectations of a hybrid origin hypothesis, and Sinclair et al. concluded that parthenogenesis originated without hybridization in *Lepidophyma* (the first such case reported in natural populations of vertebrates). Sinclair et al. (2010) were not able to sample all species of *Lepidophyma*, and their molecular data did not fully resolve relationships within *L. flavimaculatum*; here we include additional species and loci that provide greater resolution within *Lepidophyma*.

Microhabitat specialization is an ecological and evolutionary hallmark of *Xantusia* (Van Denburgh, 1895; Bezy, 1989a,b), and many populations are narrowly restricted to specific structural niches, such as rock crevices or interstices of plant material (such as fallen yucca logs). Ecological specialization for rock crevices also is present in five species of *Lepidophyma*, although correlated morphological specialization is less pronounced than in *Xantusia*. Vagility is low throughout Xantusiidae, and often individuals will live under the same cover object throughout much of their lives (up to a decade or more, Zweifel and Lowe, 1966; Fellers and Drost, 1991; Mautz, 1993). This low vagility fosters extensive population structuring and independent evolution of morphologies correlated with microhabitats, which may sometimes confound efforts at species delimitation (Sinclair et al., 2004; Leavitt et al., 2007); on the other hand, it better preserves phylogenetic signals, which are less subject to being overridden by contemporary gene flow (Cruzan and Templeton, 2000; Pfenniger and Posada, 2002). A phylogeny based on robust character and taxon sampling should provide deeper insights into the origin of different ecomorphologies within *Xantusia* and *Lepidophyma*.

Xantusia riversiana is restricted to three of the California Channel Islands (San Nicolas, Santa Barbara, and San Clemente). On the basis of morphology, it differs extensively from its mainland relatives and was once placed in a separate genus (*Klauberina*; Savage, 1957, 1963), and later considered the sister group of all other *Xantusia* (review in Vicario et al., 2003). Trees based on mitochondrial DNA sequences indicate that this large-bodied species is nested within a clade whose other members are small-bodied (Hedges et al., 1991; Hedges and Bezy, 1993; Vicario et al., 2003; Sinclair et al., 2004). While such patterns would be indicitave of the evolution of insular gigantism in *X. riversiana*, relationships of this taxon are inconsistent across studies, hindering inferences concerning its evolutionary history.

1.1. Goals of study

Our primary objectives are to obtain a robust phylogenetic hypothesis of relationships within the Xantusiidae, based on the most dense character and taxonomic sampling completed to date, and use this phylogenetic hypothesis to examine the following questions: (1) What are the relationships among *Cricosaura*, *Lepidophyma*, and *Xantusia*? (2) Does the divergence of *Cricosaura* pre-date the time of separation of the Proto-Greater Antilles from the mainland and the time of the KT asteroid impact? (3) Is the origin of unisexuality in *Lepidophyma* best explained as two events (as hypothesized by Sinclair et al., 2010), or a single event, with or without reversal? (4) How many times have rock-crevice ecomorphs evolved in Xantusiidae? And (5) what are the relationships of the island endemic *X. riversiana* to all other *Xantusia*?

2. Materials and methods

2.1. Taxon sampling

This study is based on an ingroup taxon sample of 154 specimens spanning the geographic and taxonomic diversity of Xantusiidae, and including 31 of the 34 currently recognized species. Despite extensive collecting effort, tissues for two species of *Lepidophyma* (*L. chicoasensis* and *L. tarascae*) were unavailable, as were samples from the recently described *L. zongolica* (García-Vázquez et al., 2010). While the number of species within *Xantusia* is still not fully resolved (Leavitt et al., 2007), we include terminals representing all 14 currently recognized species (Bezy et al., 2008) plus two genetically distinct but undescribed lineages identified by Leavitt et al. (2007). Multiple individuals were sequenced for most ingroup species (in some cases upwards of 20 individuals) to quantify the sometimes extensive diversity within clades (Sinclair et al., 2004; Leavitt et al., 2007). Outgroup sampling includes 20 squamates representing broad sampling within Scleroglossa based

Table 1
Oligonucleotide amplification and sequencing primers used for the 11 mitochondrial and nuclear gene regions included in this study and the original citation for each. Positions with mixed bases are labeled with standard IUPAC ambiguity codes: K = G or T, M = A or C, R = G or A, V = A or C or G, Y = T or C, and N = any base.

Primer name	Primer Sequence (5′ → 3′)	Citation
Mitochondrial primers		
Cytochrome *b*		
Cytb L1	TGA TAT GAA AAA CCA TCG TTG	Palumbi, 1996
Cytb R2	GGG TGR AAK GGR ATT TTA TC	Palumbi, 1996
Cytb F1	TGA GGA CAR ATA TCH TTY TGR GG	Whiting unpubl.
Cytb RD	GGT TTA CAA GAC CAG TGC TTT	Morando unpubl.
ND4		
ND4 f	CAC CTA TGA CTA CCA AAA GCT CAT GTA GAA GC	Arevalo et al., 1994
ND4leu	CAT TAC TTT TAC TTG GAT TTG CAC CA	Arevalo et al., 1994
16S		
16SL	CGC CTG TTT AAC AAA AAC AT	Kocher et al., 1989
16SH	CCG GTC TGA ACT CAG ATC ACG T	Kocher et al., 1989
12S		
tPhe	AAA GCA CRG CAC TGA AGA TGC	Wiens et al. (1999)
12e	GTR CGC TTA CCW TGT TAC GAC T	Wiens et al. (1999)
Nuclear primers		
BDNF		
BDNF-F	GAC CAT CCT TTT CCT KAC TAT GGT TAT TTC ATA CTT	Noonan and Chippindale, 2006
BDNF-R	CTA TCT TCC CCT TTT AAT GGT CAG TGT ACA AAC	Noonan and Chippindale, 2006
C-MOS		
C-MOS G73	GCG GTA AAG CAG GTG AAG AAA	Saint et al., 1998
C-MOS G78	AGR GTG ATR GCA AAV GAR TAR ATG	Saint et al., 1998
NT3		
NTF3 F1	ATG TCC ATC TTG TTT TAT GTG ATA TTT	Noonan and Chippindale, 2006
NTF3 R3	TTA CAY CKY GTT TCA TAA AAA TAT T	Noonan and Chippindale, 2006
RAG-1		
RAG-1 Mart FL1	AGC TGC AGY CAR TAY CAY AAR ATG TA	Hoegg et al., 2004
RAG-1 Amp R1	AAC TCA GCT GCA TTK CCA ATR TCA	Hoegg et al., 2004
Alpha enolase		
EnolLL731	TGG ACT TCA AAT CCC CCG ATG ATC CCA GC	Friesen et al., 1997
EnolH892	CCA GGC ACC CCA GCT TAC CTG GTC AAA	Friesen et al., 1997
Gapdh		
GapdL890	ACC TTT AAT GCG GGT GCT GGC ATT GC	Friesen et al., 1997
GapdH950	CAT CAA GTC CAC AAC ACG GTT GCT GTA	Friesen et al., 1997
POMC		
POMC-1	GAA TGT ATY AAA GMM TGC AAG ATG GWC CT	Wiens et al., 2005
POMC-2	TAY TGR CCC TTY TTG TGG GCR TT	Wiens et al., 2005

on recent syntheses of squamate relationships (Wiens et al., 2010, 2012; Mulcahy et al. 2012) and two iguanians (Estes et al., 1988; Gauthier et al., 1988a,b; Lee, 1998, 2005; Reynoso, 1998; Lee and Caldwell, 2000; Evans, 2003).

2.2. Character sampling

In total, 11 gene regions were sequenced for this study, including mitochondrial and nuclear loci that in combination provided phylogenetic signal capable of resolving relationships across the range of divergence times represented by our ingroup sample. We used four mitochondrial regions (the small subunit 12S [972 bp] and 16S [584 bp] ribosomal genes, and the NADH dehydrogenase 4 [ND4; 672 bp] and cytochrome *b* [cyt-*b*; 1143 bp] protein-coding genes), and seven nuclear regions (alpha-enolase [AE; 256 bp], oocyte maturation factor [c-mos; 495 bp], proopiomelanocortin-A gene [POMC; 627 bp], brain derived neurotrophic factor [BDNF; 711 bp], glyceraldehyde-3-phosphate dehydrogenase [GAPDH; 167 bp], neurotrophin-3 [NT3; 531 bp], recombination activating-1 gene [RAG-1; 840]). For most ingroup terminals, these 11 loci provided an average of 7186 bp of aligned sites. Table 1 lists the primers used for amplification and sequencing of these regions.

Total genomic DNA was extracted from muscle or liver tissue with a DNeasy extraction kit (Qiagen Inc., Valencia, CA) following manufacturer's protocols. DNA templates and controls were amplified in 25 μl reactions using standard PCR techniques. All products were visualized on 2% agarose gels. Products were amplified with TaKaRa Hotstart Taq DNA polymerase and subsequently purified with the Montage PCR96 Filter Plate Kit (Millipore Co., Bedford, MA). Sequencing reactions were performed with the Applied Biosystems Big Dye version 3 cycle sequencing kit, and purified with Sephadex in MultiScreen Durapore PVDF plates (Millipore Co., Bedford, MA). Purified products were directly sequenced on an ABI 3100 automated sequencer. To ensure the accuracy of sequences, negative controls were included and complementary strands were sequenced. Sequences were edited and contigs were assembled with Sequencher 3.1.1 (Gene Codes Corp., Ann Arbor, MI). We were successful in obtaining complete sequences for most of the 174 taxa included in this analysis; however, a few taxa lack one or more genes or portions of genes, particularly specimens with poor DNA quality. We discontinued our efforts only after repeated attempts failed to yield sequence data for these individuals. In six cases involving outgroups for which we could not obtain c-mos sequences, and one for which we could not obtain an ND4 sequence, we used data for species from GenBank that have traditionally been assigned to the same genera to create a composite terminal. Sequences were deposited in GenBank; accession numbers are listed in Appendix I.

2.3. Alignment and phylogenetic analyses

Preliminary alignments of all genes were performed with ClustalX 1.64 (Thompson et al., 1997) using default parameters (gap opening = 10; gap extension – 0.20; delay divergent sequences = 30%; DNA transition weight = 0.50) with adjustments made by eye to minimize the number of indels. MacClade 4.0 (Maddison and Maddison, 2005) was used to translate protein-coding sequences into amino acids to verify the codon reading frame and check for stop codons. All protein coding gene alignments were unambiguous with few indels present in the final alignments. Alignment of the relatively more quickly evolving ribosomal (e.g., 12S and 16S rRNA) gene regions was slightly more complicated. Following preliminary alignment with ClustalX using default parameters (see above) these alignments were "fine-tuned" by eye (in MacClade) to maximize blocks of sequence identity to stem regions (Kjer, 1995) inferred from secondary structure models (Gutell et al., 1994; http://www.rna.icmb.utexas.edu). All alignments have been deposited in the Dryad Repository: http://dx.doi.org/10.5061/dryad.011n0.

Initially, nonparametric bootstrap analyses in PAUP* (Swofford, 2002) were used to analyze each gene region for strongly supported incongruence with other gene trees. Comparing nonparametric bootstrap (BS) support for nodes of individual gene trees allowed assessment of strongly supported incongruence among data subsets (following Wiens, 1998). Conflict between gene trees might result from differences in coalescent histories, recombination (in nuclear sequences), non-orthology, or human error, and following Benavides et al. (2007), we take the absence of strongly-supported conflict to indicate that these potentially confounding factors do not seriously influence the topologies of the gene genealogies used in this study.

In order to infer relationships within Xantusiidae, we performed Bayesian analyses of a subset of taxa including all xantusiids and their sistergroup (Cordylidae + Gerrhosauridae; Mulcahy et al. 2012). Three Bayesian analyses were performed on the combined data sets employing: (1) a single model (GTR + I + Γ) across all data; (2) one model per locus; and (3) a different model applied to each codon position or different structural areas of ribosomal genes (e.g., stems vs. loops). In the latter two analyses, we employed DTModsel to select the appropriate model of gene evolution for each gene fragment and partition (Minin et al., 2003). A comparison of Bayes factors was employed to evaluate performance of the different partitioning strategies (Brandley et al., 2005; Wiens et al., 2005). Bayesian phylogenetic analyses were performed with MrBayes v3.2.1 (Ronquist et al., 2012) with model parameter values treated as unknown and estimated in each analysis. Random starting trees were used and analyses were run for a minimum of 20 million generations. In all analyses, four Markov chains were used with the temperature profile at the default setting, trees were sampled every 1000 generations, and the majority rule (50%) consensus trees and posterior probabilities for nodes derived from the post burn-in sample. Burn-in was determined by viewing plots of log-likelihoods over time provided by viewing the sump output in Tracer (v1.2; Rambaut and Drummond, 2003). All analyses were run on the BYU cluster Marylou4. (http://marylou.byu.edu/m4/marylou4.htm) or the CIPRES portal (www.phylo.org; Miller et al., 2010), and convergence of topologies and parameters was checked by running a minimum of two replicate searches for each separate and combined data set.

Where relevant, we tested our best-supported hypotheses against alternatives with different topologies (i.e., one vs. two origins of unisexuality) using the Shimodaira and Hasegawa tests (S–H test; Shimodaira and Hasegawa, 1999) in PAUP*. The null hypothesis in this test is that the alternative tree topology being compared to our best-supported hypothesis is not significantly different in its support given the data, and rejection of the null indicates a significant difference in tree topologies. Parsimonious inference of ecomorph evolution was reconstructed in MacClade.

2.4. Molecular divergence time calculations

Molecular data provide a means of estimating divergence times between taxa, as the genetic divergence between them is a product of the substitution rate and time. In order to obtain temporal estimates of the divergence of xantusiids we employed a Bayesian relaxed molecular clock with uncorrelated rates (BEAST 1.7; Drummond and Rambaut, 2003) and fossil-based calibrations and related priors. The development of relaxed clock methods for inferring divergence times has progressed rapidly in the last decade (Sanderson, 1997; Thorne et al., 1998; Drummond et al., 2002; Drummond and Rambaut, 2007), as have methods in which prior information (e.g., plate tectonic or fossil) may be incorporated in

these analyses in the form of age constraints. Though early implementations of these methods imposed such calibrations as fixed ages (Sanderson, 1997) or uniform priors from a minimum age to infinity (Thorne et al., 1998), more recent methods make better use of prior knowledge by allowing the prior to take various distributions (e.g. normal, lognormal, exponential; Drummond et al., 2006).

The appropriate use of available distributions on prior constraints was reviewed by Ho (2007), who concluded that the lognormal distribution is generally the most suitable for fossil-based calibrations. In such cases, it is assumed that the origin of a clade is earlier than its first appearance in the fossil record. Exponential priors are less suitable for fossil constraints (the prior probability decreases exponentially as time increases) due to the incomplete nature of the fossil record and the high likelihood that the first fossil of a group does not accurately represent the actual time of origin. Normal distributions are similarly unsuitable for fossil based calibrations, as they do not act as a minimum age (see Fig. 1g of Ho, 2007).

Eight fossil calibrations were used to place priors on the age of nodes within our tree (Table 2). Prior information on clade ages derived from fossil material was implemented as the lower limit of a lognormal distribution on the age of the node at the base of the smallest crown clade containing that fossil on our tree. As noted by Ho (2007), the main difficulty in implementing lognormal prior distributions in relaxed clock analyses is the number of parameters (mean, standard deviation) other than lower limit (fossil age) required. Furthermore, the lower limit must be chosen with care as paleontological literature, from which fossil calibrations are drawn, focuses on horizons (spanning millions of years) while calibration bounds require a single point for a lower limit (Parham and Irmis, 2008; Near et al., 2008). In these analyses the lower limit is the most recent age of the reported horizon from which the fossil was reported (Table 2). As we had little prior knowledge to guide our choice of mean and standard deviation for the lognormal priors on constrained node ages, we conducted analyses with multiple values for both mean (1.0, 2.0) and standard deviation (SD) (1.0, 2.0).

With an expanded dataset including 20 non-xantusiid, squamate outgroups and a topology constrained by patterns inferred in recent comprehensive analyses of squamate phylogeny (Mulcahy et al., 2012; Wiens et al., 2012), allowing only the relationships among xantusiids to vary, the loci cyt-*b*, ND4, POMC, BDNF, c-mos, NT3 and RAG-1 were used to estimate the chronology of xantusiid divergences. For these analyses we assumed a GTR + I + Γ model of nucleotide substitution (see above), an uncorrelated lognormal model of rate variation, and a Yule prior on branching rates. Although xantusiid placement within Squamata has been contentious for some time, recent results from the Squamate Tree of Life project have resolved the relationships among all clades represented in our dataset. The results of three independent, 10 million generation analyses (sampling every 2000 generations) were compared and combined in Tracer 1.4 (Rambaut and Drummond, 2003), and LogCombiner 1.4.6. In order to ascertain the true "joint prior" of the temporal constraints used in the BEAST analysis, and thus test the strength of signal in our data, we conducted one analysis (for each combination of mean and SD) with no sequence data in our data matrix (e.g. only "???").

In two instances (calibrations 2, 3; Table 2), the fossils clearly apply to more recent divergences than can be calibrated with our taxon sampling. To assess whether the use of these fossils to calibrate older nodes adversely affected posterior estimation of divergence times, we conducted an additional analysis with corrected lower age limits applied to these nodes. These corrrected calibrations were derived from the ratio of previously estimated ages of the relevant nodes. Application of a constraint to the node uniting *Dipsosaurus* and *Gambelia* based on *Armandisaurus* (13.6 Ma) would be more appropriately applied to the younger node uniting *Dipsosaurus* and *Sauromalus* or *Brachylophus* (neither of which are included in our study). Similarly, a minimum age of 60.2 Ma applied to the node uniting *Blanus* and *Lacerta* would be more appropriately applied to the younger node uniting *Blanus* and *Rhineura*. As recent analyses of divergence times within other squamate clades have included both nodes, we were able to apply corrected calibrations based on the ratios of the relevant node ages estimated in those studies (Vidal and Hedges 2005; Wiens et al., 2006; Townsend et al., 2011). The ratios of estimated ages (youngest node:sampled node) resulted in corrected calibrations of 26 Ma for node 2 (*Armandisaurus*) and 65.2 Ma for node 3 (*Plesiorhineura*). It should be noted that these corrections are based on the relative depths of the two nodes in previous studies and do not depend on the correctness of the estimated values.

Because of its age and inferred phylogenetic relationships, one of the most important and controversial fossils referred to Xantusiidae is the Middle Paleocene *Paleoxantusia fera*. Although the age of this taxon is well documented, its phylogenetic placement has been questioned. *Paleoxantusia fera* has been employed in a number of molecular based estimates of xantusiid divergence times, but the placement of this calibration has varied among studies (Vicario et al., 2003; Roca et al., 2004; Hedges, 2006). Based on preliminary analyses of the phylogenetic placement of *P. fera*, which suggest it is a stem *Xantusia* (Gauthier, pers. comm.), we have the age of this fossil (60.2 Ma) as a lower age limit on the node reflecting the *Cricosaura* – *Xantusia*/*Lepidophyma* split. When attempting to answer the lingering question of pre-KT presence (and asteroid survival) of Antillean xantusiids it is important to realize that this placement of *P. fera* largely precludes the possibility of a post Cretaceous origin (stem age) of *Cricosaura*. Thus, in order to be conservative in our analysis (accounting for the possibility of incorrect placement and/or incorrect dating of this fossil), we also have run analyses with only seven fossil-based constraints (excluding the *P. fera* calibration) to assess how much this constraint contributes to the inferred age of the earliest divergence among extant xantusiids.

Table 2
Eight calibration points (employed simultaneously) used in BEAST analysis of divergence time. Calibrations were enforced as a lognormal prior on the node indicated (Fig. 4).

Calibration (node)	Min. time estimate	Fossil	Reference
1: MRCA of *Boa* and *Gambelia*	93.5 My	*Haasiophis*, *Euopodophis*, *Pachyrhachis*	Longrich et al. 2012
2: MRCA of *Dipsosaurus* and *Gambelia*	13.6 My	*Armandisaurus*	Norell and de Queiroz 1991
3: MRCA of *Blanus* and *Lacerta*	60.2 My	*Plesiorhineura*	Sullivan 1985
4: MRCA of *Boa* and *Xantusia*	140.0 My	*Paramacellodus*	Gauthier et al. 2012
5: MRCA of *Cricosaura* and *Xantusia*	60.2 My	*Paleoxantusia fera*	Estes 1983
6: MRCA of *Lepidophyma* and *Xantusia*	55.0 My	*Paleoxantusia sp* CG	Smith 2009
7: MRCA of *Cricosaura* and *Cordylus*	89.3 MY	*Utahgenys*	Nydam and Fitzpatrick 2009
8: MRCA of *Coleonyx* and *Hemidactylus*	54.0 My	*Yantarogekko*	Bauer et al. 2005

Table 3
Characteristics of the 11 gene regions used for this study. Range of uncorrected pairwise distance (upd) is given as a basic comparison of genetic variation across genes and has been standardized by comparing the same taxa across all genes. For exemplar intrageneric, intrafamilial, and ingroup–outgroup upd ranges, a comparison was made between *Lepidophyma pajapanense* 542 and *L. smithii* 035, *L. smithii* 035 and *Cricosaura* 547842, and *L. smithii* 035 and *Lacerta* YPM 12858, respectively. For genes where only a subset of taxa were sequenced (i.e., 18S and 28S), an alternative taxon was used. Best-Fit ML models and parameters were determined by Bayesian models as determined by DT-ModSel (Minin et al., 2003).

Partition (number of terminals)	Characters (no. pars. inf.)	Intrageneric Upd	Intrafamilial Upd	Ingroup-outgroup Upd	ML model	Bayesian model	Prop. of inv. sites (I)	Gamma-shape parameter	Ti:Tv ratio
MtDNA									
12S (61) for *Lepidophyma* only	969 (371)	0.189	n/a	n/a	GTR + I + G	GTR + G	0.2418	0.5072	3.2785
16S (169)	584 (268)	0.132	0.273	0.334	GTR + I + G	TrN + I + G	0.2599	0.4052	2.5067
cyt-*b* (175)	1143 (682)	0.202	0.275	0.318	GTR + I + G	GTR + I + G	0.3207	0.7337	3.4708
ND4 (175)	672 (456)	0.191	0.448	0.475	GTR + I + G	GTR + I + G	0.2272	0.6051	3.5581
Nuclear									
A Enolase (158)	260 (98)	0.009	0.290	0.112	HKY + G	HKY + I	0.0000	0.3861	1.8645
BDNF	755 (58)	0.008	0.170	0.384	K81uf + I + G	K80 + I + G	0.5884	0.8395	2.3686
c-mos (175)	495 (236)	0.020	0.119	0.228	HKY + I + G	HKY + I + G	0.3280	3.2623	2.1961
Gapdh (143)	355 (183)	0.047	0.259	n/a	TVM + I + G	HKY + I + G	0.2039	0.9425	2.0526
NT3 (175)	531 (219)	0.008	0.067	0.164	TVM + I + G	K81 + G	0.2225	1.5513	2.3568
POMC (175)	627 (238)	0.011	0.204	0.326	GTR + I + G	TrN + G	0.3755	0.9405	1.7295
RAG-1 (167)	898 (273)	0.004	0.322	0.637	GTR + I + G	TVMef + I + G	0.4945	0.4944	2.0131

3. Results

3.1. Patterns of sequence variability

Our molecular matrix includes 7186 nucleotides of aligned sequence data (3090 parsimony-informative sites) from four mitochondrial and seven nuclear gene regions. Table 3 summarizes patterns of variation for each gene region (e.g., size of the sequence, number of terminals sequenced, and the number of parsimony-informative characters). The mitochondrial cyt-*b*, ND4, 12S and 16S loci were the most variable within genera, whereas the nuclear BDNF and RAG-1 genes were the least variable. In comparisons between the outgroup and the ingroup taxa, RAG-1 was the most variable locus for which outgroup data were available.

The best-fit model for each gene sequenced for this study was selected by DTModsel (Minin et al., 2003) and is reported in Table 3. Independent Bayesian analyses converged on similar ln-likelihood scores and generation times; the first 150,000 generations were discarded as burn-in. Bayesian and parsimony (bootstrap) analyses yielded largely concordant results for most analyses including those of the individual gene trees (not illustrated), and differences generally involved nodes that were only weakly supported (e.g., $\leqslant$50% BS) by one or more methods. Most clades present in separate gene trees also were present in the combined data tree but with higher support values in the combined data tree. No highly-supported conflicts were found between any combination of gene trees, so all further phylogenetic analyses were carried out on concatenated data sets.

3.2. Molecular phylogeny of the Xantusiidae

Our analyses of relationships within Xantusiidae are based on four mitochondrial and seven nuclear regions, which varied considerably in their degree of divergence across taxa incorporated in this study (Table 3). The combined DNA data resulted in nearly congruent results inferred by all methods of analysis (Figs. 2 and 3). In addition, most nodes received relatively high (e.g., >0.95 Bayesian posterior probability [BPP]) support. In all analyses of combined DNA data, *Cricosaura* is recovered (BPP = 1.0) as sister to (*Lepidophyma* + *Xantusia*; BPP = 1.0), with each of these genera strongly supported as monophyletic (BPP = 1.0). Relationships within *Xantusia* are largely congruent with those reported by Leavitt et al. (2007), though relationships among larger clades (deeper nodes) differ substantially. This is almost certainly due, in part, to the rooting constraints employed by Leavitt et al. (2007). We performed S–H tests to compare our inferred tree (*Cricosaura* (*Lepidophyma* + *Xantusia*) with constraint trees conforming to previously proposed hypotheses: *Lepidophyma* (*Cricosauraa* + *Xantusia*) and *Xantusia* (*Cricosaura* + *Lepidophyma*) (the hypotheses of Conrad (2008) and Crother et al. (1986), respectively). Our inferred tree is significantly better, given our data, than these other hypotheses ($P < 0.001$ for both tests).

Our findings support the monophyly of three major clades of *Xantusia*: the insular *X. riversiana*, a southern clade (*X. bolsonae*, *X. extorris*, *X. sanchezi*, *X. gilberti*, *X. sherbrookei*, *X. gracilis*, *X. henshawi*), and a northern clade (*X. arizonae*, *X. jaycolei*, *X. sierrae*, *X. vigilis*, *X bezyi*, *X. wigginsi*) (Fig. 2). Consistent with the results of Sinclair et al. (2004), the species of *Xantusia* are found to be monophyletic, except that *X. sierrae* appears to have been derived from within *X. vigilis*. Our sampling did not permit testing of the hypothesis of Lovich (2001) that *X. gracilis* was derived from within *X. henshawi*. Our results differ from those of Sinclair et al. (2004) and are congruent with those of Leavitt et al. (2007) in finding that *X. bezyi* is sister to (*X. wigginsi* + the 'San Jacinto' + 'Yucca Valley' clades), whereas *X. vigilis* is the sister taxon of (*X. arizonae* + *X. jaycolei*).

Within *Lepidophyma*, the combined DNA tree contains four moderately supported major clades (Fig. 3): (1) a southern clade composed of six species (*L. flavimaculatum*, *L. reticulatum*, *L. lipetzi*, *L. tuxtlae*, *L. mayae*) and an undescribed species from Chiapas, Mexico (*Lepidophyma* sp. ENEPI 5793-4 in Fig. 3); (2) a northern clade (*L. occulor*, *L. sylvaticum*, and *L. micropholis*) sister to (3) a Tehuantepec clade composed of (a) small-bodied, rock-crevice species (*L. dontomasi*, *L. radula*, *L. lowei*, and *L. cuicateca*), and (b) large-bodied non-rock-crevice species (*L. smithii* and *L. lineri*). The relationships of both *L. gaigeae* (poorly supported) and *L. pajapanense* (unresolved) with respect to the aforementioned clades are not clearly resolved by our data. The species recognized by Bezy and Camarillo (2002) are monophyletic with three exceptions: *L. sylvaticum* is paraphyletic relative to the cave-dwelling *L. micropholis*; *L. smithii* as presently circumscribed is paraphyletic relative to *L. lineri*; and two specimens (terminals *Lepidophyma* sp. ENEPI 5793-4) identified morphologically as *L. flavimaculatum* by Bezy and Camarillo (2002), are consistently placed outside that species and appear to represent a previously unrecognized species.

3.3. Divergence time estimates for Cricosaura typica

Consistent with previous findings (Roca et al., 2004; Hedges, 2006), our estimate of the timing of divergence of the Caribbean *Cricosaura typica* from the mainland xantusiids

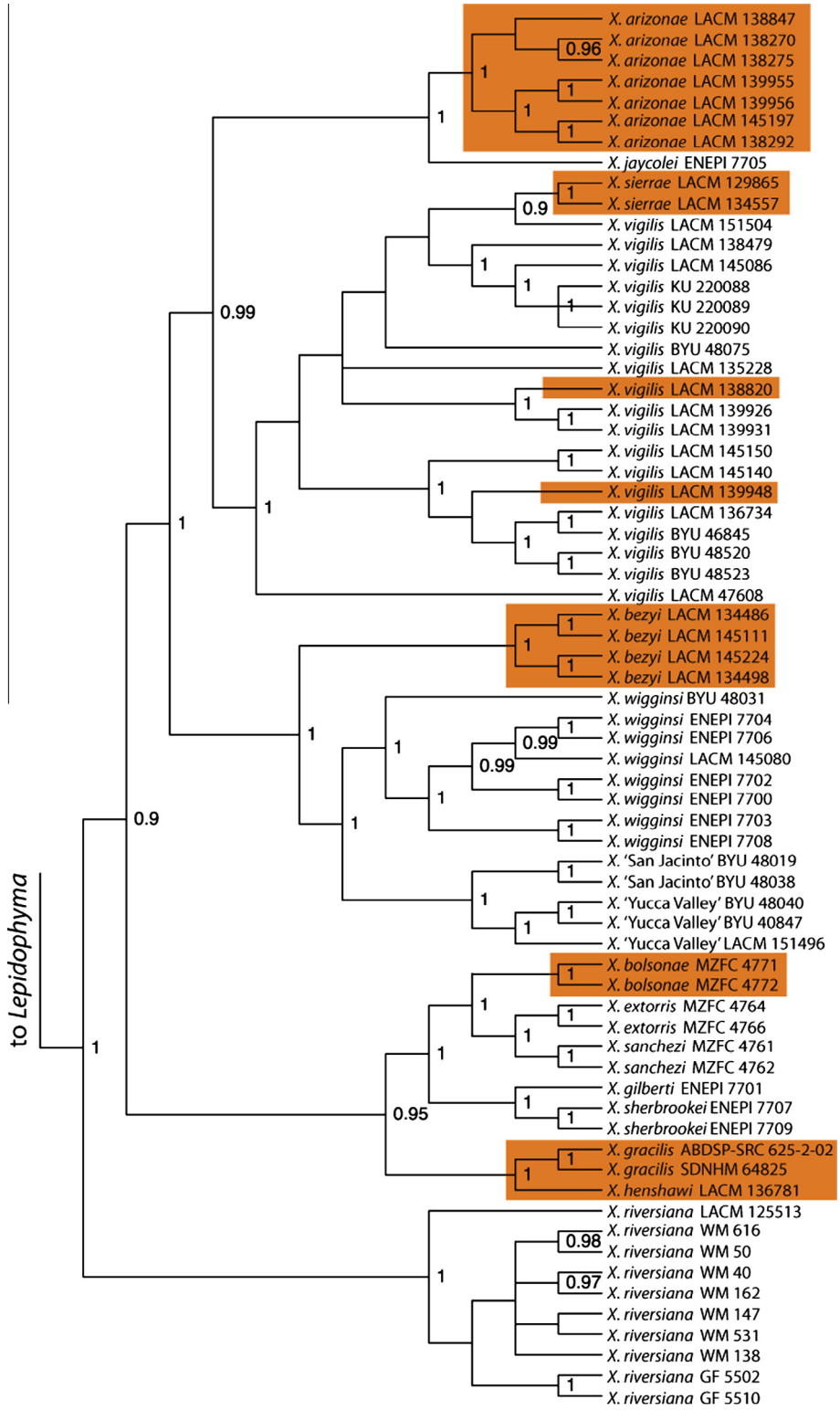

Fig. 2. Bayesian consensus tree showing relationships within *Xantusia*; the inset indicates the illustrated portion of the xantusiid tree with branch lengths proportional to amounts of change. For ease of inclusion of support values, an ultrametric tree is shown. Orange boxes indicate terminals having a rock-crevice ecomorphology. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(*Xantusia* + *Lepidophyma*) falls entirely within the Mesozoic (81 Ma, 68–93; mean and 95% HPD respectively) (Fig. 4). Our assessment of the sensitivity of posterior distributions to different lognormal parameters on node constraints (various combinations of means [1, 2] and standard deviations [1, 2]) indicates that these had little effect on results (Fig. 5).

Analyses employing adjusted calibrations for nodes 2 and 3 (Table 2) had a greater effect on the inferred age of *Cricosaura*, but still placed it firmly in the Mesozoic (76 Ma, 67–86). Notably, these corrections had little effect within Episquamata, where they were applied (including the nodes that they were used to calibrate), but they resulted in decreased age estimates (~5 million

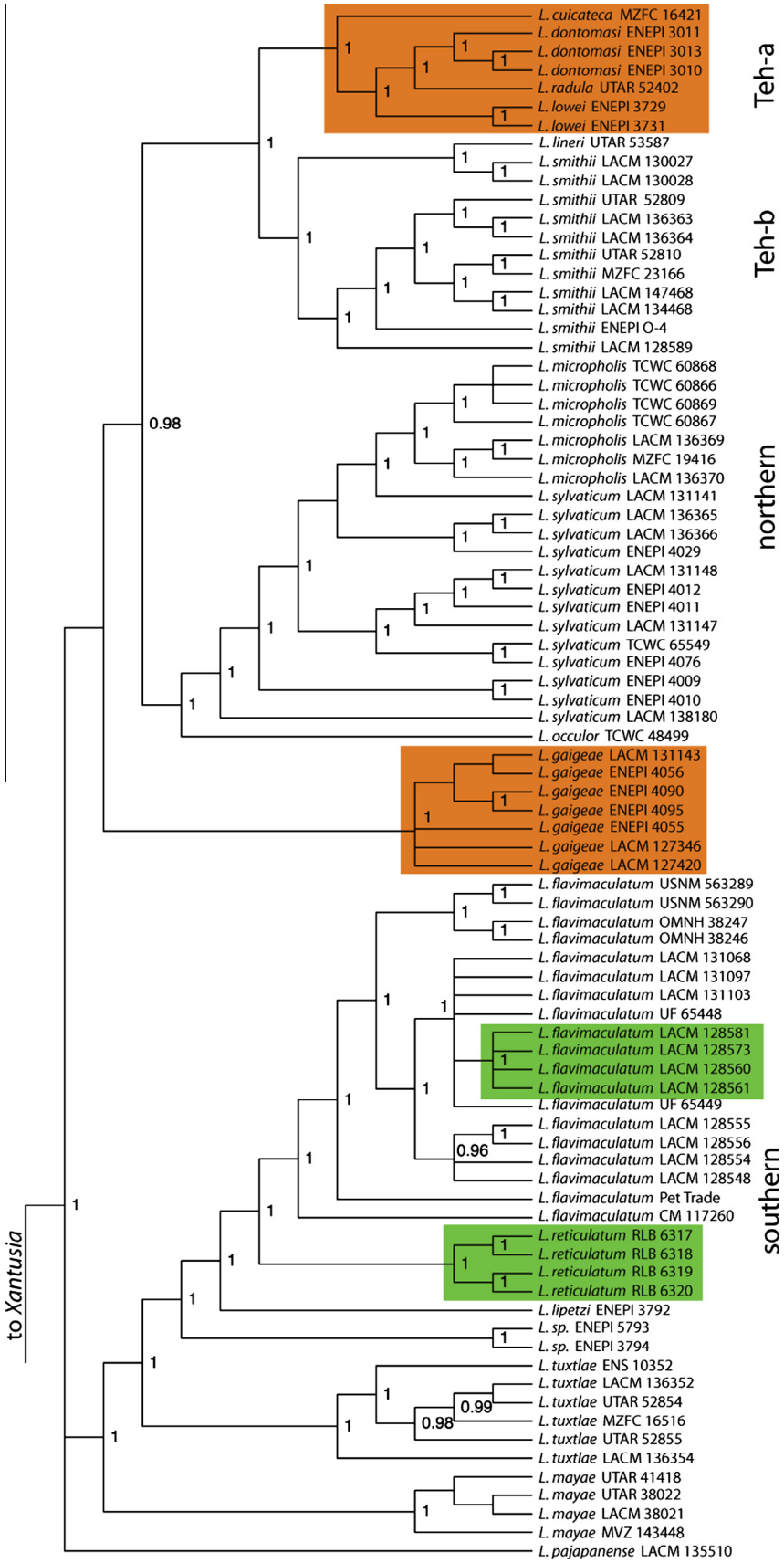

Fig. 3. Bayesian consensus tree showing relationships within *Lepidophyma*; the inset indicates the illustrated portion of the xantusiid tree with branch lengths proportional to amounts of change. For ease of inclusion of support values, an ultrametric tree is shown. Colored boxes indicate terminals having a rock-crevice ecomorphology (orange) and unisexual reproduction (green). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

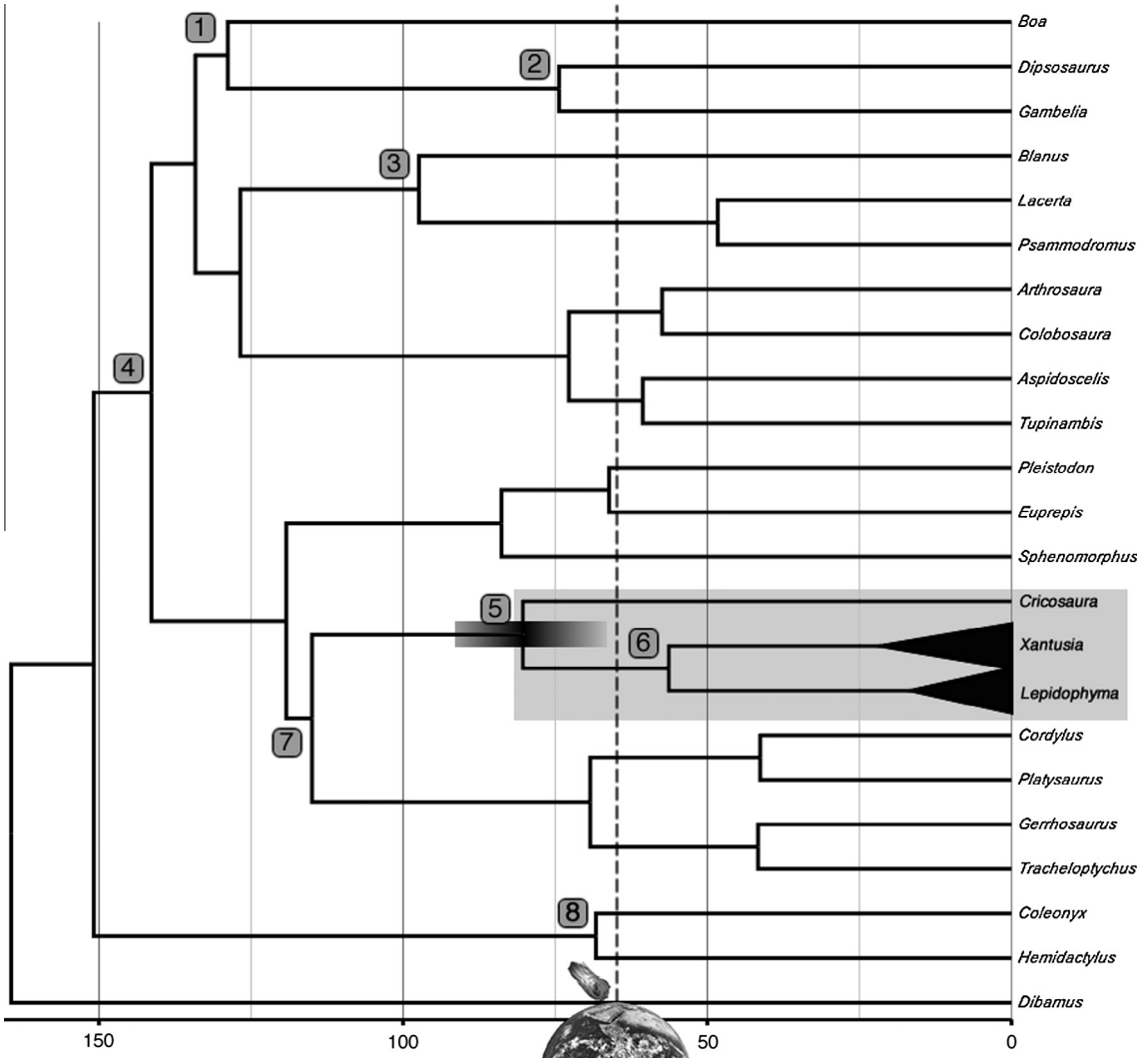

Fig. 4. Bayesian consensus tree illustrating divergence time estimates within Xantusiidae (results from analysis with lognormal priors on calibrated nodes, mean and standard deviation = 1; assuming an uncorrelated lognormal relaxed clock; scale on *x*-axis in Ma). Numbered nodes are based on fossils summarized in Table 2, and shaded bars represent 95% credibility intervals. Estimates place the origin of *Cricosaura* at 78 Ma, consistent with vicariance resulting from tectonic divergence of the Greater Antilles and predating the end-Cretaceous mass extinction (dashed line and Earth impact illustrate the timing of the onset of this event).

years (My)) for deeper nodes within Scincoidea, including the divergence of *Cricosaura*. In addition, although the corrected calibrations assigned older minimum ages to nodes 2 and 3, the analysis employing the corrected calibrations estimated younger ages for those nodes.

Our assessment of the influence of the *P. fera* calibration point on divergence time estimates suggests that exclusion of this calibration had little effect (~1 My) on posterior estimates of divergence times with the lone exception of the node to which the calibration was applied and the two preceding it. Posterior distributions for the *C. typica* divergence time estimates resulting from runs with and without the *P. fera* calibration all suggest a Cretaceous divergence, though the posterior estimate for this node increased by 6 My (to 87 Ma) when the *P. fera* calibration was excluded. Fig. 4 summarizes our estimate of the time of *Cricosaura* divergence, relative to the more recent splits within the Xantusiidae, in the context of the KT boundary.

3.4. Evolution of parthenogenesis and cryptic diversity within *Lepidophyma*

Fig. 3 illustrates the evolution of unisexuality in *Lepidophyma*; one instance within a single well-supported clade of *L. flavimaculatum*, and the second in a well supported clade that includes all individuals of *L. reticulatum*. The latter species is presumed to be unisexual throughout its range, and is inferred as sister to the well-supported monophyletic *L. flavimaculatum*, which includes the single unisexual and multiple gonochoristic populations. Within *L. flavimaculatum*, the gonochoristic populations are paraphyletic with respect to the unisexuals, which are deeply nested in a pectinate topology that separates *L. reticulatum* from the unisexual *L. flavimaculatum* populations by five well-supported nodes (Fig. 3). S–H tests indicated that the difference between the inferred tree and a tree with all unisexual populations of *L. reticulatum* and *L. flavimaculatum* constrained to monophyly was highly significant ($P < 0.0001$).

Although our inferred relationships among *Lepidophyma* species differ significantly from the mtDNA phylogeny of Sinclair et al. (2010), those relationships largely conform to the pattern inferred in their analysis of nuclear loci. Our findings augment the reconstruction of relationships among *Lepidophyma* by placing the previously unsampled *L. cuicateca, L. lineri,* and *L. sp.*. We also find *L. sylvaticum* to be strongly structured, showing deep splits among populations from different localities, and support the paraphyly of this taxon with respect to *L. micropholis*. The two species together are inferred as a well-supported

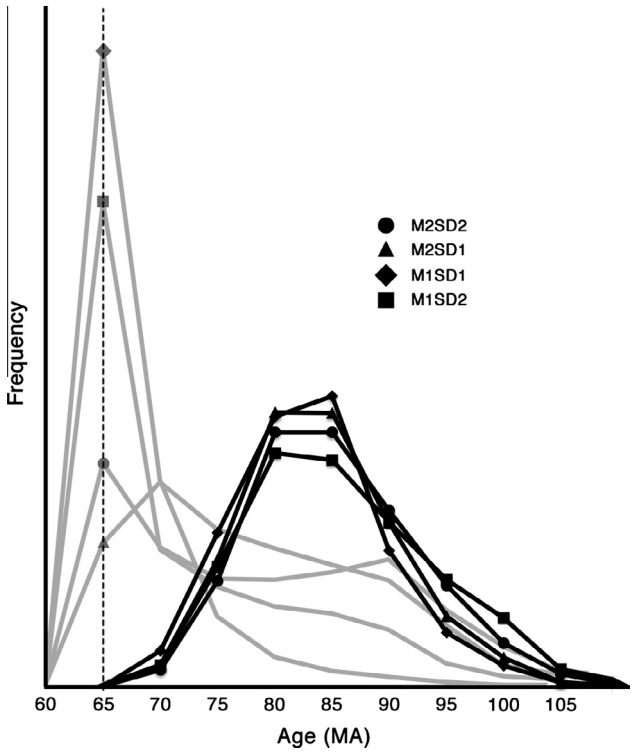

Fig. 5. Joint prior (gray) and posterior (black) distributions of divergence time estimates for the node uniting *Cricosaura* and *Xantusia* + *Lepidophyma*. Results summarize frequency (*y* axis) of divergence times (in 5 MY bins) obtained from the last eight million generations of the uncorrelated lognormal relaxed clock analyses. Vertical dashed line indicates Cretaceous/Tertiary boundary (65 Ma). Legend at bottom distinguishes results of runs with different prior distribution parameters in the form of mean (M) and standard deviation (SD).

(*L. micropholis* + *L. sylvaticum*) clade, which is corroborated as the sister clade of *L. occulor*.

We performed S–H tests to evaluate the monophyly of *L. sylvaticum* with respect to *L. micropholis*, and the monophyly of gonochoristic *L. flavimaculatum* with respect to unisexual *L. flavimaculatum*. Our hypothesis in Fig. 3 was significantly better than both of these alternatives ($P < 0.001$). Our tree also was significantly better than a tree containing a monophyletic *L. smithii* clade with respect to *L. lineri* ($P = 0.0110$).

3.5. Ecomorph evolution

Within *Xantusia*, our Bayesian consensus tree of the combined DNA data suggests multiple origins of the rock-crevice ecomorph (Fig. 2; branches leading to terminals associated with rock-crevice habitats are indicated in orange). Following Sinclair et al. (2004), we estimated the number of plant-litter to rock-crevice microhabitat transitions under a parsimony criterion, which indicated a minimum of seven independent ecomorph transitions to the rock-crevice ecomorph. These occur along the branches subtending the following nodes in *Xantusia*: (1) (*X. gracilis* + *X. henshawi*); (2) *X. bolsonae*; (3) *X. bezyi*; (4) *X. arizonae*; (5) *X. sierrae*; (6) *X. vigilis* in the Hualapai Mountains, Arizona, (LACM 138820); and (7) *X. vigilis* in the Cottonwood Mountains, Arizona (LACM 139948). S–H tests indicated there was a significant difference ($P < 0.0001$) between the inferred tree (Fig. 3) and each of three hypothetical constraint trees that assume fewer evolutionary origins of the rock-crevice ecomorph: (*X. bezyi* + *X. arizonae*); (*X. bezyi* + *X. arizonae* + *X. bolsonae*); and (*X. bezyi* + *X. arizonae* + *X. bolsonae* + *X. sierrae*).

Five species exhibit a rock-crevice ecomorphology within *Lepidophyma*: *L. gaigeae*, *L. lowei*, *L. dontomasi*, *L. radula*, and *L. cuicateca* (orange branches in Fig. 3). Although our findings do not strongly support the placement of *L. gaigeae*, it is clear that this species is no fewer than two nodes removed from the other clade of rock-crevice species (Teh-a). Thus, our findings support two origins of the rock-crevice ecomorph in *Lepidophyma* (i.e., in the ancestral lineage of *L. gaigeae* and in the most recent common ancestor of the other four species) under parsimony ancestral state reconstruction.

4. Discussion

4.1. Origin and age of Cricosaura

Since Wallace's (1881) original discussion of the fauna and flora of islands, questions concerning the origins and evolution of the distinctive Antillean biota have fascinated biogeographers. In the past few decades, three divergent, but potentially overlapping, biogeographic models have been proposed for the origins of the Antillean vertebrate fauna (reviews in Iturralde-Vinent and MacPhee, 1999; Fontenla, 2006; MacPhee and Iturralde-Vinent 2005; Hedges, 2006; Echeverry 2011). The continent-island vicariance model of Rosen (1975) placed a major emphasis on a Cretaceous origin of the biota associated with the formation of the proto-Greater Antillean Arc and its subsequent eastward drift relative to North and South America. Hedges and co-workers (Haas et al., 1993; Hedges, 2006) have inferred that the dates of divergence of endemic Antillean clades of amphibians and reptiles from mainland species, as estimated largely from immunological distances, are not clustered in the late Cretaceous and early Paleocene and are generally younger than expected on the basis of Rosen's model. They have postulated over water dispersal consistent with the present northeast tending currents extending from the Atlantic coast of South America to the Antilles. Iturralde-Vinent and MacPhee (1999) examined the geology, paleontology, and oceanography of the Caribbean region and concluded that: (1) there is no evidence that any Antillean area has remained continuously subaerial throughout the Cenozoic; (2) past currents provided a means to deposit waifs from South America preferentially onto the Gulf Coast of Central America rather than on the Antilles; and (3) dispersal to the Antilles from South America may have been facilitated by an Eocene–Oligocene landspan hypothesized for the period of maximal land exposure at ca 35–33 Ma.

In view of the existence of these alternative biogeographic models, it is important to ascertain whether any exclusively Antillean vertebrate stem lineages date from (or prior to) the time of separation of the proto-Greater Antillean arc from North America (ca 70–75 Ma) using independent lines of evidence. Analyzing allozymes, Hedges (1996) dated the separation of Caribbean *Eleutherodactylus* frogs from their mainland relative as 70 ± 6.8 Ma (Late Cretaceous). However, more recently Heinicke et al. (2007), using sequence data and relaxed-clock divergence time methods, have estimated this divergence as 47 (35–65) Ma, which is not consistent with a Cretaceous origin. Based on sequences from 16 nuclear and three mitochondrial genes, Roca et al. (2004) also employed relaxed-clock methods to place the divergence of the Antillean endemic *Solenodon paradoxus* from mainland eulipotyphlan insectivores at 76 Ma (72–81 Ma), thus leaving this divergence consistent with Cretaceous vicariance (but see discussion of problems of dating relictual clades, below).

Utilizing partial sequences from three mitochondrial genes and the 60 Ma fossil *Paleoxantusia fera*, Hedges et al. (1991) and Hedges and Bezy (1993) concluded that the divergence of the Cuban endemic xantusiid lizard *Cricosaura typica* from *Xantusia*—*Lepidophyma* of mainland North America may have dated from the Cretaceous or earlier. Vicario et al. (2003) excluded *P. fera* as a calibration, and using the next oldest fossils (43 and 15 Ma) and the same three partial sequences concluded that the divergence of *Cricosaura* from

its mainland sister group was post-Cretaceous, dating to 65–43 Ma. Based on these identical sequences, but using different dating methods, Roca et al. (2004) and Hedges (2006) re-calculated the divergence estimate for *Cricosaura* as 76 (57–101) Ma.

In this study, utilizing sequences from five nuclear and two mitochondrial loci (BDNF, c-mos, NT3, POMC, RAG-1, cyt-*b*, and ND4) and eight fossil calibrations, our estimate for the divergence of *Cricosaura* from *Xantusia* + *Lepidophyma* is 81 (68–93) Ma. We thus conclude that *Cricosaura* diverged from other extant xantusiids at around the time the proto Geater Antillian arc separated from North America, and prior to the end-Cretaceous mass extinction.

Problems with applying biogeographic models to relictual clades such as *Solenodon* and *Cricosaura* were discussed recently by Hedges (2006) and Heinicke et al. (2007). Dispersal of *Cricosaura* to the Antilles does not seem likely to have occurred via the hypothesized Eovene-Oligocene landspan as there is no evidence that xantusiids ever occurred in South America. In light of the claim that no area on the Antilles has remained subaerial throughout the Tertiary (Iturralde-Vinent and MacPhee, 1999; MacPhee and Iturralde-Vinent, 2005), there are at least two alternative hypotheses for the history of *Cricosaura*, both of which reflect our finding that its age is consistent with separation of the proto–Greater Antilles from Middle America. The first is that *Cricosaura* has continuously occupied the landmass that currently comprises southeastern Cuba, and that the claim that no part of the Antilles has been subaerial throughout the Tertiary is incorrect. Alternatively, Tertiary submersion of all Antillean landmasses may be correct, in which case either *Cricosaura* dispersed more recently to southeast Cuba, with subsequent extinction of mainland relatives more closely related to it than to *Lepidophyma* and *Xantusia*, or the taxon has been present on the Antilles since their formation, but its position has shifted from one subaerial land mass to another.

Despite these unresolved biogeographic issues, our divergence time estimates support the hypothesis that *Cricosaura* originated before and survived the Chicxulub KT impact (65 Ma). The buffered micro-habitats occupied, preference for low body temperatures, and low metabolic rate of xantusiids would appear to make them good candidates for survival through the catastrophic climatic changes of this event.

4.2. Origin of unisexual Lepidophyma and cryptic diversity within this genus

The nuclear, mitochondrial, and combined data trees all strongly support the independent origin of the unisexual reproductive mode (presumed parthenogenesis) in *L. reticulatum* and within *L. flavimaculatum*. We have corroborated the topology reported by Sinclair et al. (2010), on the basis of more inclusive taxonomic and character sampling, but unlike the earlier study, our larger data set provides greater phylogenetic resolution within *L. flavimaculatum* (Fig. 3). Sinclair et al. considered the alternative possibility of a single origin of parthenogenesis in the common ancestor of *L. flavimaculatum* and *L. reticulatum*, followed by a reversal back to sexual reproduction in the ancestor of the bisexual populations of *L. flavimaculatum*. This interpretation was made somewhat tenable by the low resolution of population relationships within *L. flavimaculatum* in their study (Sinclair et al., 2010; their Fig. 3), but our finding of the strongly supported, deeply nested position of the unisexual populations makes this explanation unlikely.

Sinclair et al. (2010) found moderate levels of microsatellite heterozygosity in *L. reticulatum* compared to complete homozygosity of unisexual *L. flavimaculatum*, suggesting that the former is of greater age. The congruence of trees for nuclear and mitochondrial genes is consistent with a non-hybrid origin of these parthenogens, and detailed site-by-site comparisons among the nuclear sequences and among 14 microsatellite loci for all populations of *L. flavimaculatum* and *L. reticulatum* yield no evidence that either of the two unisexuals are of hybrid origin (Sinclair et al., 2010).

One other observation of note here is that although most of the currently recognized species of *Lepidophyma* are well-supported as monophyletic, often a reflection of deep phylogenetic splits, *L. smithii* and *L. sylvaticum* are found to be paraphyletic with respect to *L. lineri* and *L. micropholis* respectively. Given the deep splits and cryptic diversity that characterize *Xantusia* (Sinclair et al., 2004; Leavitt et al., 2007), these observations in widely distributed species of *Lepidophyma* are not surprising and suggest that cryptic diversity is hidden in the current taxonomy.

4.3. Ecomorphological evolution

Xantusia populations inhabiting rock-crevices differ from those in yuccas in having relatively larger and flatter bodies, longer limbs, more boldly spotted color patterns, and higher numbers of scales for several meristic characters (Bezy, 1967, 1989a,b; Vicario et al., 2003; Sinclair et al., 2004; Fig. 6). We use the terms "rock-crevice ecomorph" and "yucca ecomorph" based on structural niche and morphology, but recognize that some populations referred to the yucca ecomorph are found in other decaying plants, including agaves, nolinas, sotols, and cardón, pine, mesquite, and oak logs. In spite the array of plants inhabited, representatives of

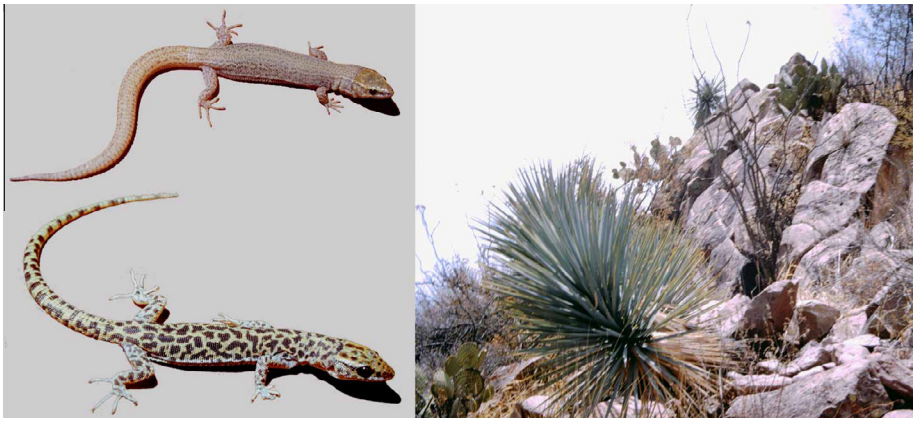

Fig. 6. Sympatric species of *Xantusia* in Durango, Mexico, illustrating differences in morphology associated with structural niche. *X. bolsonae* (lower left, rock-crevice ecomorph, SVL 50 mm) occurs in andesite boulders (right); *X. extorris* (yucca ecomorph, upper left, SVL 40 mm) occurs in adjacent decaying yuccas and agaves. Phylogenies derived from both mitochondrial and nuclear DNA sequences indicate that the rock-crevice ecomorph has evolved multiple times in *Xantusia*.

the yucca ecomorph are remarkably similar in general morphology and habitus and their small body size is suited for life inside decaying yuccas and agaves. Five species (*X. henshawi*, *X. gracilis*, *X. bolsonae*, *X. bezyi*, and *X. arizonae*) are considered to represent a high degree of adaptation to the rock-crevice habitat based on the magnitude of their morphological specializations. *Xantusia sierrae* and the rock-crevice inhabiting populations of *X. vigilis* are more weakly differentiated in morphology from lizards that inhabit yucca, and in a few populations individuals are found in both plants and rock-crevices without morphological differences. *Xantusia sanchezi* is labeled as a plant inhabiting species on the basis of our samples from the type locality in Zacatecas (where it was found under mesquite bark), although populations have recently been discovered inhabiting rock-crevices in Jalisco.

When the evolution of ecomorphic features is reconstructed on our inferred tree, ecomorphic features appear to be highly plastic in *Xantusia*, where a large number of evolutionary transitions are inferred, but directionality remains unclear. Considering only two ecomorph states, parsimony-based ancestral state reconstructions on our tree suggest that transitions occurred from yucca to rock-crevice ecomorph, rather than vice versa and that the rock-crevice ecomorph evolved 7 times. If only the extreme rock-crevice ecomorph is considered (excluding *X. sierrae* and *X. vigilis*) the rock-crevice ecomorph is again inferred to be derived, with 4 independent evolutionary origins.

There are additional factors that would seem to favor multiple origins of the rock-crevice ecomorph. The populations in question differ in the degree of their morphological specialization for inhabiting rock crevices, are geographically highly isolated, and occupy stationary geologic features not expected to have been continuous in the past. Members of the yucca ecomorph have a more uniform morphology, are more widely distributed, and live in plants with ranges that fluctuate with climatic change and thus previously may have been more continuously distributed. It is also possible, however, that *Xantusia* was not as highly confined to particular structural niches early in its history as it is today, and may have evolved in response to Cenozoic climatic changes through the derivation of both yucca and rock-crevice ecomorphs from a more generalized ancestral condition (Vicario et al., 2003).

Within *Lepidophyma*, morphological specialization for rock-crevices appears to have evolved twice: in *L. gaigeae* and in the clade composed of *L. dontomasi*, *L. radula*, *L. lowei*, and *L. cuicateca*. Compared to other *Lepidophyma*, members of the rock-crevice ecomorph have a smaller body size, tubercular scales that are smaller and usually lack keels, caudal whorls that are less differentiated in size, scale surfaces with a distinctive micro-structure, and fewer scales on several parts of the body (Bezy and Camarillo, 2002; Bezy and Peterson, 1988; Canseco-Márquez et al., 2008). *Lepidophyma gaigeae* is the most extreme in the above morphological features and occurs almost exclusively in limestone crevices in the Sierra Madre Oriental (Taylor, 1939; Dixon et al., 1972; Bezy and Camarillo, 1992). The other four species occur primarily in rock-crevices, but sometimes are found under rocks on the ground and in decaying plants (Bezy and Camarillo, 1997; Canseco-Márquez et al., 2008).

4.4. Phylogenetic position of Xantusia riversiana

Originally described as a member *Xantusia* by Cope in 1883, the island endemic *X. riversiana* was placed in the genus *Klauberina* by Savage (1957) as it is phenotypically divergent from other living xantusiids (Savage, 1963; Crother et al., 1986; Vicario et al., 2003; Gauthier et al., 2008). In previous analyses based exclusively on sequences from mitochondrial genes, the large-bodied *X. riversiana* has been consistently found to be nested within clades of otherwise small-bodied species of *Xantusia* (Hedges et al., 1991; Vicario et al., 2003; Sinclair et al., 2004; Leavitt et al., 2007), contrary to morphological interpretations.

Analysis of nuclear genes has sometimes succeeded in reconciling differences between phylogenies based on morphology and those based on mitochondrial sequences, particularly when lateral gene transfer via hybridization or incomplete lineage sorting may have occurred (e.g., Leaché and McGuire, 2006; McGuire et al., 2007). The mitochondrial, nuclear, and combined DNA trees for *Xantusia* strongly support *Xantusia* as monophyletic. Our analysis of relationships within Xantusiidae provides moderate (BPP = 0.9) support for *X. riversiana* as sister to the rest of *Xantusia*, consistent with earlier phylogenies based exclusively on morphology.

Xantusia riversiana is one of the few species of vertebrates endemic to the California Channel Islands that has a high level of divergence (both molecular and morphological) from its mainland relatives. How long the species has been isolated on the islands is of considerable importance for understanding the historical biogeography of the California coastal borderland (reviewed in Bezy et al., 1980). Leavitt et al. (2007) have estimated the divergence of *X. riversiana* at 13.8 my (Miocene), a number consistent with our estimate (16 My, 6–32). Given that the outer California Channel Islands may have been connected to the Baja California Peninsula in the Miocene (Crouch, 1979), a period almost entirely included in our posterior estimate, the isolation of *X. riversiana* on the islands may be a consequence of subsequent northward drift of the islands (Crother et al., 1986). Evidence of Pleistocene submergence for Santa Barbara and San Nicolas Islands (Vedder and Howell, 1980) precludes the continuous persistence of *X. riversiana* on these two islands since the Miocene. However, marine terraces evidencing submergence do not extend to the summit of San Clemente Island, and thus *X. riversiana* could have survived on this island during the Pleistocene and subsequently dispersed to San Nicolas and Santa Barbara Islands.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2013.05.017.

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