

# Phylogeny, divergence times and species limits of spiny lizards (*Sceloporus magister* species group) in western North American deserts and Baja California

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## Abstract

The broad distribution of the *Sceloporus magister* species group (squamata: phrynosomatidae) throughout western North America provides an appropriate model for testing biogeographical hypotheses explaining the timing and origins of diversity across mainland deserts and the Baja California Peninsula. We inferred concordant phylogenetic trees describing the higher-level relationships within the *magister* group using 1.6 kb of mitochondrial DNA (mtDNA) and 1.7 kb of nuclear DNA data. These data provide strong support for the parallel divergence of lineages endemic to the Baja California Peninsula (*S. zosteromus* and the *orcutti* complex) in the form of two sequential divergence events at the base of the *magister* group phylogeny. A relaxed phylogenetic analysis of the mtDNA data using one fossil and one biogeographical constraint provides a chronology of these divergence events and evidence that further diversification within the Baja California clades occurred simultaneously, although patterns of geographical variation and speciation between clades differ. We resolved four major phylogeographical clades within *S. magister* that (i) provide a novel phylogenetic placement of the Chihuahuan Desert populations sister to the Mojave Desert; (ii) illustrate a mixed history for the Colorado Plateau that includes Mojave and Sonoran Desert components; and (iii) identify an area of overlap between the Mojave and Sonoran Desert clades near Yuma, Arizona. Estimates of bidirectional migration rates among populations of *S. magister* using four nuclear loci support strong asymmetries in gene flow among the major mtDNA clades. Based on the nonexclusivity of mtDNA haplotypes, nuclear gene flow among populations and wide zones of phenotypic intergradation, *S. magister* appears to represent a single geographically variable and widespread species.

*Keywords:* biogeography, dating, gene flow, migration, phylogeography, relaxed phylogenetics

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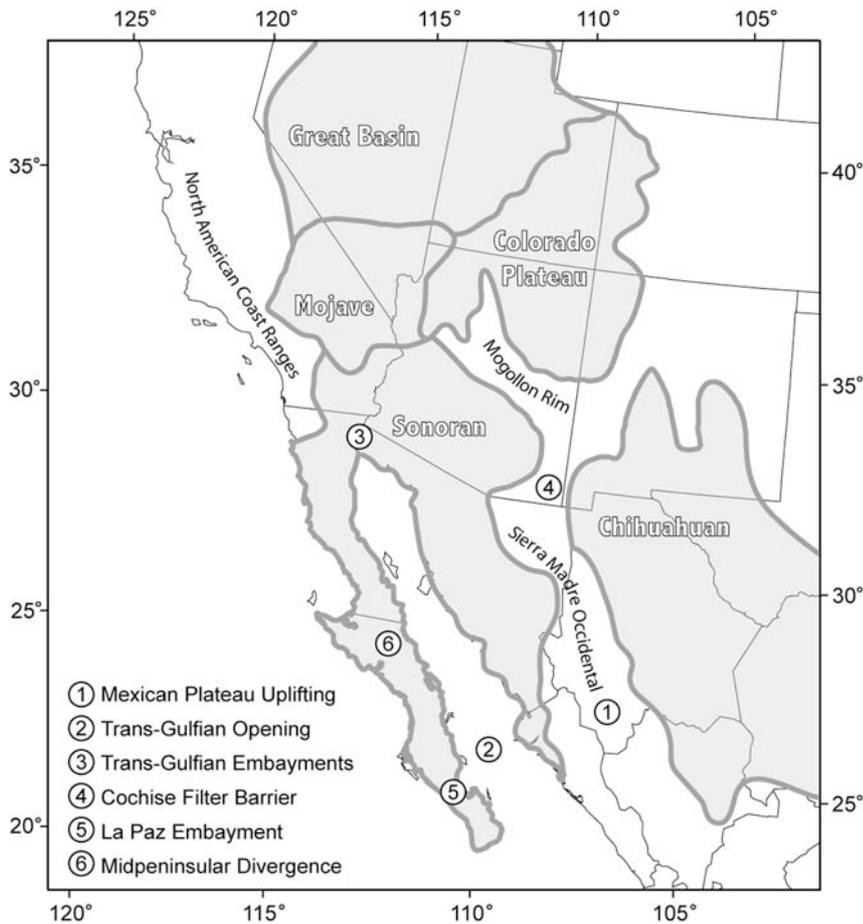
## Introduction

Alternative hypotheses explaining the historical biogeography and diversification of the western North American desert biota are beginning to approach a generalized model. In place of strict dispersal scenarios that were pervasive prior to the establishment of plate tectonic theory (e.g. Savage 1960) are more appropriate vicariance and dispersal models that

are supported by multitaxon comparisons of gene trees (Riddle & Hafner 2006). However, novel vicariance hypotheses continue to be proposed as different lineages are examined, particularly with more complete taxonomic and geographical sampling. Estimating divergence times for a taxonomic group with a broad distribution and a sharp concordance between phylogenetic breaks and the location of arid region junctions (Fig. 1) can provide a chronology for the evolution of the western North American desert biota.

Dating divergence events on a phylogenetic tree is straightforward when nucleotide substitutions occur in a clock-like manner and a credible molecular rate calibration is

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**Fig. 1** Approximate distributions of the major western North American deserts and the location of the key geographical features considered responsible for the diversification and evolution of the modern desert biota.

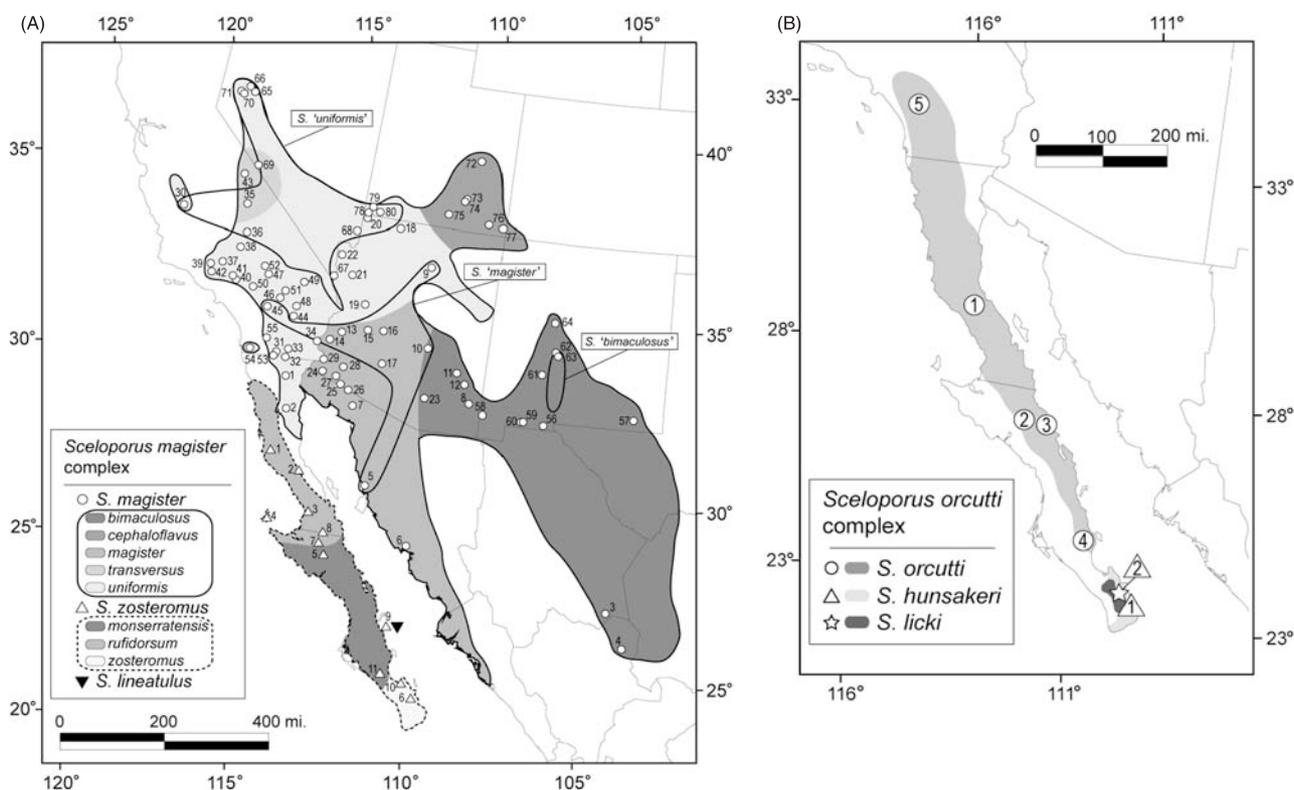
available (Thorne & Kishino 2005). However, the assumption of rate constancy is violated by most data sets, and converting units of molecular evolution to an externally calibrated timescale remains a challenge for taxa with poor fossil records (Arbogast *et al.* 2002). Relaxed molecular clock methods that allow rates to vary across the tree eliminate the requirement of rate constancy (Rutschmann 2006), and recent advances in Bayesian phylogenetics allow for probabilistic age constraint priors on nodes rather than fixed calibration points (Drummond *et al.* 2006; Yang & Rannala 2006). Incorporating uncertainty into a nodal age constraint in the form of a flexible prior distribution is appealing since age estimates from fossils or biogeographical events, which are common sources for external calibrations, are best represented by a distribution of values (Ho 2007). Relaxed Bayesian phylogenetic analyses realize the full potential of these recent advances by estimating simultaneously the phylogeny and divergence times while incorporating probabilistic calibration priors on nodes and allowing evolutionary rates to vary across the tree (Drummond *et al.* 2006).

Spiny lizards of the *Sceloporus magister* species group (the *magister* group) occupy every major western North American desert and represent the largest radiation of *Sceloporus*

lizards on the Baja California Peninsula (Murphy 1983a; Sites *et al.* 1992; Wiens & Reeder 1997). The occurrence of the *magister* group across the mainland and peninsular deserts and on deep-water islands in the Gulf of California makes it an ideal group for testing biogeographical hypotheses explaining the timing and origins of diversity on the Baja California Peninsula (Table 1). The *magister* group contains six species divided into two species complexes. The *magister* complex (Grismer & McGuire 1996; Fig. 2a) includes *S. magister* (containing five subspecies widespread in the USA and Mexico), *S. zosteromus* (containing three subspecies endemic to the Baja California Peninsula) and *S. lineatulus* (endemic to Isla Santa Catalina). High levels of geographical variation in colouration and patterning, generally restricted to adult males, are evident across the range of *S. magister* and *S. zosteromus*, with distinct populations usually showing intergradation at their contact zones (Phelan & Brattstrom 1955; Parker 1982; Grismer & McGuire 1996). The *orcutti* complex (Hall & Smith 1979), restricted to the peninsular region (Fig. 2b), includes *S. orcutti* (widespread through Baja California north of the Cape Region into southern California), *S. hunsakeri* and *S. licki* (both endemic to the Cape Region).

**Table 1** Previous hypotheses for divergence events within the *Sceloporus magister* species group

Divergence Event	Estimated Time (Ma)	Geologic Event	Reference
<i>magister</i> complex vs. <i>orcutti</i> complex	5–10	Sierra Madre/Mexican Plateau uplifting	Murphy (1983a, b)
<i>S. orcutti</i> vs. <i>S. hunsakeri</i> + <i>S. licki</i>	5.2–6.6	La Paz embayment	Murphy (1983a)
<i>S. orcutti</i> vs. <i>S. hunsakeri</i> + <i>S. licki</i>	1.6–3	La Paz embayment	Grismer (1994)
<i>S. magister</i> vs. <i>S. zosteromus</i>	6–14	Trans-gulfian opening	Welsh (1988)
<i>S. magister</i> vs. <i>S. zosteromus</i>	9.8	Trans-gulfian opening	Schulte <i>et al.</i> (2006)
<i>S. magister</i> vs. <i>S. zosteromus</i>	5	Trans-gulfian embayment	Murphy (1983a)
<i>S. magister</i> vs. <i>S. zosteromus</i>	1–3	Trans-gulfian embayment	Grismer (1994)
<i>S. zosteromus</i> : Cape Region vs. Peninsula	1.6–3	La Paz embayment	Grismer (1994)
<i>S. zosteromus</i> vs. <i>S. lineatulus</i>	2	Separation of Isla Santa Catalina from Peninsula	Murphy (1983a, b)
<i>S. zosteromus</i> : Isla Monserrate vs. Peninsula	< 2	Formation of Isla Monserrate	Murphy (1983a, b)
<i>S. magister</i> : Chihuahua vs. Mojave + Great Basin deserts	3.8	Not mentioned	Schulte <i>et al.</i> (2006)
<i>S. magister</i> : Sonora desert vs. Chihuahua + Mojave + Great Basin deserts	4.9	Not mentioned	Schulte <i>et al.</i> (2006)



**Fig. 2** Generalized distributions of taxa in the *Sceloporus magister* species group divided into (A) the *magister* complex and (B) the *orcutti* complex. Numbers correspond to sampled localities listed in Appendix I. For *S. magister* (A), we outline the geographical extent of the mtDNA-based species limits proposed by Schulte *et al.* (2006).

In this paper, we apply a variety of genetic markers, including mitochondrial DNA (mtDNA) fragments, nuclear exons and non-coding nuclear DNA (nDNA), to address questions concerning the phylogeny, divergence times, and population genetics of the *S. magister* species group. First,

we compare separate phylogenetic trees derived from the mtDNA and nuclear exon data sets for concordance. Conducting separate analyses of independent loci is advantageous because it provides a mechanism for identifying instances of incongruence caused by incomplete lineage

sorting, hybridization or introgression (Leaché & McGuire 2006). Next, we conduct a relaxed phylogenetic analysis using the mtDNA data to provide a chronology of the early and recent divergence events that occurred in the *magister* group. Based on a combination of the phylogeny and divergence times, we discuss the biogeography and diversification of the *magister* group. Finally, our dense population-level sampling of *S. magister* enables us to refine the boundaries of previously described mtDNA clades, resolve their interrelationships, discover new clades and identify areas of putative secondary contact where further studies of species limits are required. We combine the variation present in two non-coding nuclear loci with the nuclear exons to estimate migration rates between the major mtDNA clades which coincide loosely with the major desert regions. We conclude by discussing the systematics of the *magister* group and present arguments for the continued recognition of *S. magister* as a single species.

## Materials and methods

### *Taxon sampling and data collection*

All six species in the *Sceloporus magister* species group are included in our study, including all subspecies described within *S. magister* and *S. zosteromus*, with multiple individuals for most taxa (*S. hunsakeri*,  $n = 3$ ; *S. licki*,  $n = 1$ ; *S. lineatulus*,  $n = 1$ ; *S. magister*,  $n = 91$ ; *S. orcutti*,  $n = 6$ ; *S. zosteromus*,  $n = 12$ ; Appendix I). A recent study by Schulte *et al.* (2006) recognized three species within *S. magister* (*S. bimaculosus*, *S. magister* and *S. uniformis*), based primarily on the geographical fidelity of mtDNA haplotypes; however, we cannot apply this taxonomy a priori because the sparse geographical sampling employed by their study prevents us from predicting the mtDNA clade assignment of newly sampled populations. Our dense population-level sampling within *S. magister* provides increased geographical resolution for refining the boundaries and testing the exclusivity of the mtDNA-based species limits. We selected nine species of *Sceloporus* from closely related species groups to test the monophyly of the *magister* group (Appendix I). When necessary, we rooted our trees with a representative of the *variabilis* group (*S. variabilis*), which is the sister group to all remaining *Sceloporus* (Wiens & Reeder 1997; Flores-Villela *et al.* 2000).

Using polymerase chain reaction (PCR), we amplified and sequenced two fragments of mtDNA [12S ribosomal RNA (rRNA), *nad4* protein-coding gene and adjacent transfer RNA's (tRNA)] and two nuclear exons (*RAG-1*, *BDNF*) to generate estimates of phylogenetic relationships based on multiple loci. We also sequenced the non-coding nuclear loci *sun27* (ca. 575 bp) and *sun32* (ca. 500 bp) (Rosenblum *et al.* 2007) for a subset of 37 individuals within *S. magister* to provide additional data for estimating migration

rates across putative species boundaries. We downloaded two sequences from GenBank, including a *nad4* sequence for *S. magister* from Sonora, MX, and a fragment of 12S rRNA for *S. lineatulus*, which are the only molecular data available for these samples. Details of our DNA extraction, PCR, primer selection and sequencing methods are provided in Leaché & McGuire (2006).

We used the multiple sequence alignment program MUSCLE version 3.6 (Edgar 2004) to align the 12S rRNA data, and used the secondary stem-and-loop structure of the ribosomal subunit to constrain gaps to loop regions. We excluded loop regions of ambiguous alignment from subsequent analysis (Leaché & Reeder 2002). The remaining gene sequences lacked problematic indels and were imported directly into NEXUS file format for subsequent analysis. All sequences are deposited in GenBank (Accession nos EU085568–EU086049) and the mtDNA alignment and resultant phylogenetic tree are deposited in TreeBase (study Accession No. S1845).

### *Traditional phylogenetic analyses*

We reconstructed phylogeny using an unrooted likelihood-based framework under maximum likelihood (ML) and Bayesian inference. Since it is possible for the mitochondrial and nuclear genes to each have unique evolutionary histories (Moore 1995; Hudson & Turelli 2003), we evaluated separate analyses of the mtDNA and nuclear data for concordance. We conducted ML analyses using RAXML-VI-HPC version 2.1.3 (Stamatakis 2006). Our RAXML analyses implemented the GTRGAMMA nucleotide substitution model, which is equivalent to a general time-reversible model with an among-site rate heterogeneity parameter. To provide support values for inferred relationships, we implemented 2000 nonparametric bootstrap replicates. Because our mtDNA data set contains a mixture of coding and non-coding sequences, we conducted a partitioned Bayesian analysis using MRBAYES version 3.1.2 (Ronquist & Huelsenbeck 2003) with the following four partitions: 1: non-coding 12S rRNA gene and tRNAs; 2–4: first, second and third codon positions for *nad4*, respectively (Brandley *et al.* 2005). We used the Akaike information criterion in MRMODELTEST version 2.2 (Nylander 2004) to determine the best-fit nucleotide substitution model for each data partition. We produced posterior probability distributions by allowing four incrementally heated Markov chains (using default heating values) to proceed for  $2 \times 10^7$  generations, with sampling occurring every  $1 \times 10^3$  generations. We assessed convergence by inspecting the cumulative posterior probabilities of clades using AWTY (Wilgenbusch *et al.* 2004). We discarded burn-in samples from the separate analyses and combined the remaining samples to produce a 50% majority rule consensus tree with bipartition frequencies equal to posterior probability values (Huelsenbeck & Ronquist 2001).

### Relaxed phylogenetic analysis

We conducted relaxed phylogenetic analyses using BEAST version 1.4.3 (Drummond & Rambaut 2006) to simultaneously implement probabilistic prior distributions on node ages, allow evolutionary rates to vary across the tree and account for uncertainty in the phylogeny. Low levels of variation in the nuclear genes prevented us from using these data to date recent divergences within species; therefore, we restricted our relaxed phylogenetic analysis to the mtDNA data. To expedite our divergence-dating analysis, we only analyzed unique sequences.

The presence of *S. magister* throughout southwestern North America during the late Pleistocene is well established (Brattstrom 1953; Cole & Van Devender 1976), but until these fossils can be unambiguously placed on our intraspecific genealogy we cannot use them to constrain node ages. Many extant genera of phrynosomatid lizards are present in the fossil record by the early Miocene, including the first appearance of *Sceloporus* (Holman 1970; Robinson & Van Devender 1973; Yatkola 1976; Holman 1995). Therefore, we constrained the age of *Sceloporus* to correspond to 25 million years ago (Ma). We accounted for uncertainty in the age of *Sceloporus* by sampling from a broad prior distribution that extends into the late Palaeocene (60 Ma), which corresponds to the first appearance of Iguania in North America (Holman 1995). We conducted three separate analyses implementing uniform (25–60 Ma), normal (mean = 25 Ma, SD = 1.0) and log-normal (zero offset = 22 Ma, SD = 1.0) prior distributions on the root. Under each of these prior distributions, we recorded the inferred ages of *Sceloporus*, the *magister* group, the *magister* and *orcutti* complexes, each species in the *magister* group, and the major divisions within species. We prefer the assumptions implied when using a log-normal distribution for fossil age constraints on the root node, which include: (i) origination should not post-date the fossil occurrence; (ii) high probability is centred on the fossil age; and (iii) the probability of divergence decreases at older times. We placed a second age constraint on the divergence between populations of *S. zosteromus* on the Baja California Peninsula and Isla Monserrate in the Gulf of California. Isla Monserrate is a deep-water island composed of Miocene volcanic rocks covered by Pliocene limestone and Pleistocene gravels (Carreño & Helenes 2002). Although the exact age of the island is uncertain, geological (Gastil *et al.* 1983; Carreño & Helenes 2002) and biological (Murphy 1983a, b) data suggest that the island originated during the Pleistocene. To accommodate the inherent uncertainty of the age of Isla Monserrate in our divergence dating analysis, we used a normal distribution (mean = 2 Ma, SD = 1.0) for the divergence between the island and mainland populations.

For our BEAST analyses, we implemented the uncorrelated log-normal model of rate variation because it better

accommodates clock-like data and produces smaller highest posterior densities compared to alternative models (Drummond *et al.* 2006). We employed a Yule process speciation prior for the branching rates and applied the GTR + I +  $\Gamma$  model of nucleotide substitution with four rate categories. We ran our MCMC analyses for  $2 \times 10^7$  generations, logged every 1000 steps and recorded the divergence time for nodes of interest at the same frequency. We recursively reran our analyses to refine the weight and tuning operators for maximum efficiency using the auto-optimize function. After fine-tuning our analysis, we ran two separate analyses and used TRACER version 1.2 to determine convergence, measure the effective sample size of each parameter, and calculate the mean and 95% highest posterior density interval (HPD) for divergence times (Rambaut & Drummond 2004).

### Gene-flow estimation

We utilized the *RAG-1*, *BDNF*, *sun27*, and *sun32* nuclear loci to quantify gene flow across putative species boundaries within *S. magister*. We conducted comparisons between the *magister* (Sonoran Desert) + *bimaculosus* (Chihuahuan Desert) and *magister* (Sonoran Desert) + *uniformis* (Mojave and Great Basin Deserts) mtDNA clades. We estimated the following demographic parameters in a Bayesian framework in the program IM (Isolation with Migration: Hey & Nielsen 2004): effective population size of each population and the ancestral population ( $\theta_1$ ,  $\theta_2$  and  $\theta_A$ ), asymmetrical migration rates ( $m_1$  and  $m_2$ ), and the time of population splitting ( $t$ ). To ensure that our sampling reflected the stationary distribution of interest, we initiated two analyses with different starting points, incorporated 20 concurrent chains per analysis with geometric heating ( $g_1 = 0.9$  and  $g_2 = 0.8$ ) and monitored the effective sample size from each analysis as a proxy for autocorrelation. Since our analyses include autosomal nuclear genes, we assigned an inheritance scalar of 1.0. We applied the HKY model of nucleotide substitution (Hasegawa *et al.* 1985) to accommodate for multiple substitutions at a single nucleotide site and unequal base frequencies. We used the following settings for the prior distributions: scalars for theta max  $\theta_1$  and  $\theta_2 = 10$  and  $\theta_A = 30$ ; maximum migration rates  $m_1$ ,  $m_2 = 100$ ; and maximum time of population splitting  $t = 20$ .

We rescaled parameter estimates to demographic units using the geometric mean of the assumed mutation rates of the four loci under study (Won & Hey 2005). Our estimates for the mutation rates for each gene are based on the observed substitutions rates (multiplied by the length of the gene) converted to units of time, using the inferred divergence times between populations of *S. magister* obtained from our BEAST analysis (see Results). Assuming a generation time of two years for *S. magister* (Parker & Pianka 1973), we obtained a measure of mutation rate on a scale of generations.

### Ancestral area reconstructions

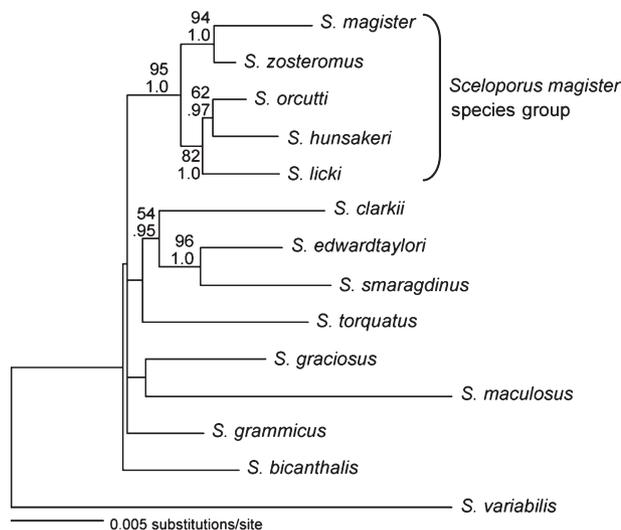
We used unordered parsimony in MACCLADE version 4.08 (Maddison & Maddison 2000) to reconstruct the ancestral areas and geographical associations between desert regions in *S. magister*. We coded individuals into seven discrete areas, including the Chihuahuan Desert, Cochise Filter Barrier, Colorado Plateau, Great Basin, Mojave Desert, North American coast ranges (NACR) and Sonoran Desert (Appendix I). To optimize character-state changes on the mtDNA genealogy, we used delayed transformation (DELTRAN) and accelerated transformation (ACCTRAN). We resolved polytomies in the mtDNA genealogy in a fashion that minimized the number of inferred ancestral state changes.

## Results

### Traditional unrooted phylogenetic analyses

The *RAG-1* nuclear gene included 1043 nucleotide positions, with 27 parsimony-informative and 112 parsimony-uninformative variable sites. The *BDNF* gene included 670 positions, with 5 parsimony-informative and 26 parsimony-uninformative variable sites. The best-fit nucleotide substitution models selected for the nuclear and mtDNA data partitions by the Akaike information criterion are provided in Appendix II. The ML and Bayesian analyses of the combined nuclear data (1713 bp) provide strong support for a sister-group relationship between the *Sceloporus magister* and *S. orcutti* complexes (Fig. 3). Significant support for a sister-group relationship between *S. magister* and *S. zosteromus* is provided by both methods as well. Within the *orcutti* group, our analysis provides strong support for a sister-group relationship between *S. orcutti* and *S. hunsakeri*, a novel topological relationship that disrupts the monophyly of the Baja California Cape endemic species *S. hunsakeri* and *S. licki*.

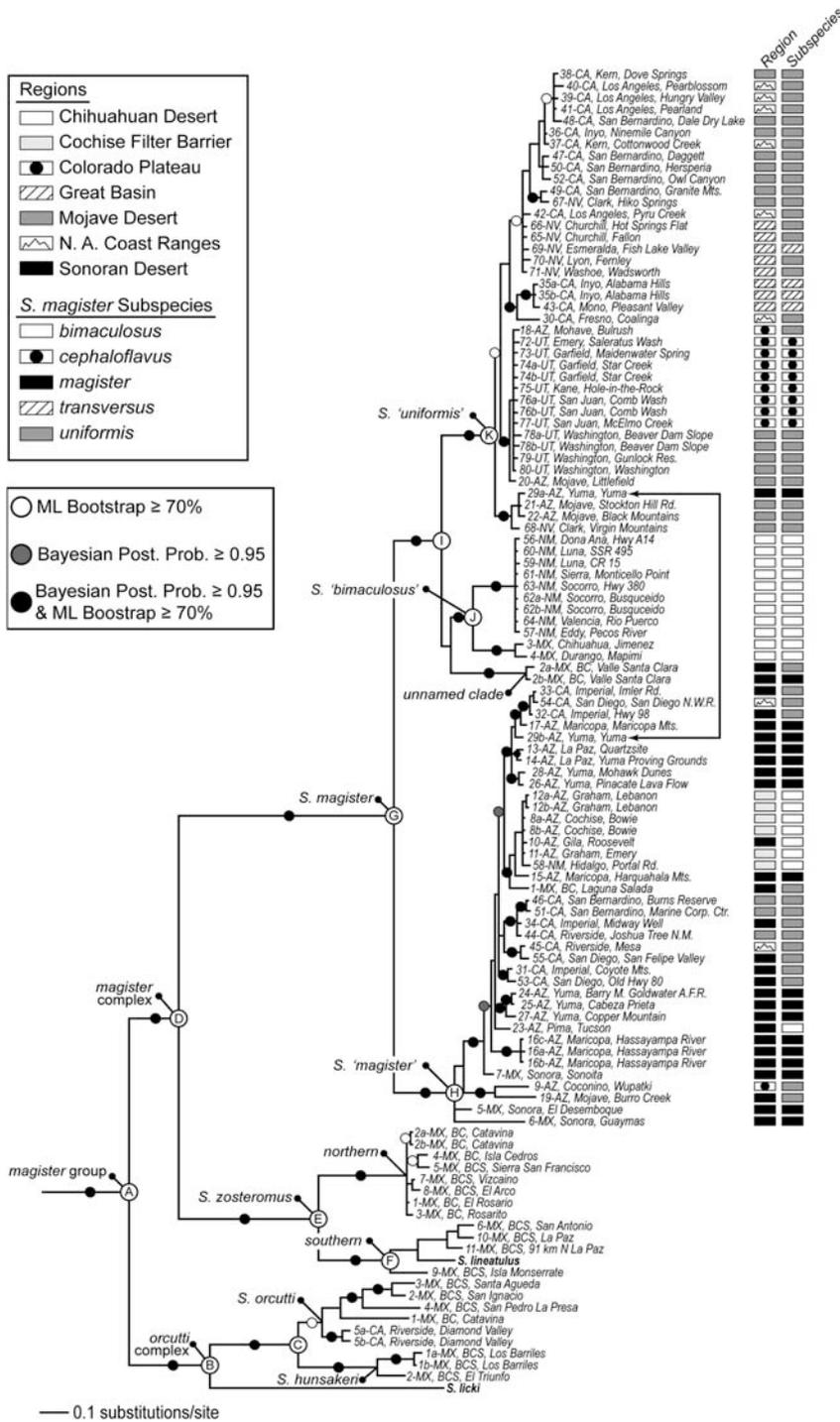
The 12S rRNA data included 781 aligned nucleotide positions, 40 of which were excluded due to ambiguous alignment. The combined mtDNA data set (including 12S, *nad4* and tRNAs) contained 1606 aligned nucleotide positions, 460 of which were parsimony-informative. ML and Bayesian phylogenetic analyses of the combined mtDNA data produced a species-level phylogeny for the *magister* group (Fig. 4) that is congruent with the higher-level relationships supported by the nuclear data (Fig. 3). The mtDNA genealogy provided resolution for population-level relationships within *S. orcutti*, *S. zosteromus* and *S. magister* (Fig. 4). Within *S. orcutti*, an initial division separated samples at the northern end of the range in California from the remaining samples in Baja California. *Sceloporus zosteromus* is divided into two main groups corresponding to northern and southern Baja California. Isla Monserrate



**Fig. 3** Maximum likelihood (ML) phylogeny for the *Sceloporus magister* species group based on a combined analysis of the *RAG-1* and *BDNF* nuclear genes (1713 bp). Numbers on branches denote ML bootstrap values (top) and Bayesian posterior probability values (bottom).

was placed sister to the southern clade, although with weak support (Fig. 4). Interestingly, the Santa Catalina Island endemic, *S. lineatulus*, is nested among samples from southern Baja California, which renders *S. zosteromus* paraphyletic. Similar to previous studies (Orange 1997; Schulte *et al.* 2006), we recovered three major clades within *S. magister* congruent with the Chihuahuan, Sonoran and Mojave + Great Basin Deserts (Fig. 4). However, contrary to other studies, we recovered a Colorado Plateau clade that is placed within the Mojave + Great Basin Deserts. Additionally, a basal lineage containing two individuals from Locality 2 in Baja California, Mexico (Fig. 4) is not assignable to any of the species proposed by Schulte *et al.* (2006) and represents a new unnamed mtDNA clade.

Within *S. magister*, we identified one instance of mtDNA nonexclusivity with respect to samples from Yuma, AZ, which were nested in the *magister* and *uniformis* clades. These mtDNA clades were separated by as little as 32 km in the Mojave Desert between sample Locality 44 and 48. A gap of ca. 75 km separated the *magister* and *bimaculosus* mtDNA clades in southwestern New Mexico (Fig. 5a). The average genetic diversity of the nDNA was low within *S. magister* (uncorrected P-distances: *RAG-1* = 0.00265; *BDNF* = 0.00023; *sun27* = 0.00632; *sun32* = 0.00219) compared to the mtDNA (uncorrected P-distance = 0.06541), resulting in the failure of the nuclear data to differentiate any of the major mtDNA clades within *S. magister* with strong support (Fig. 5).

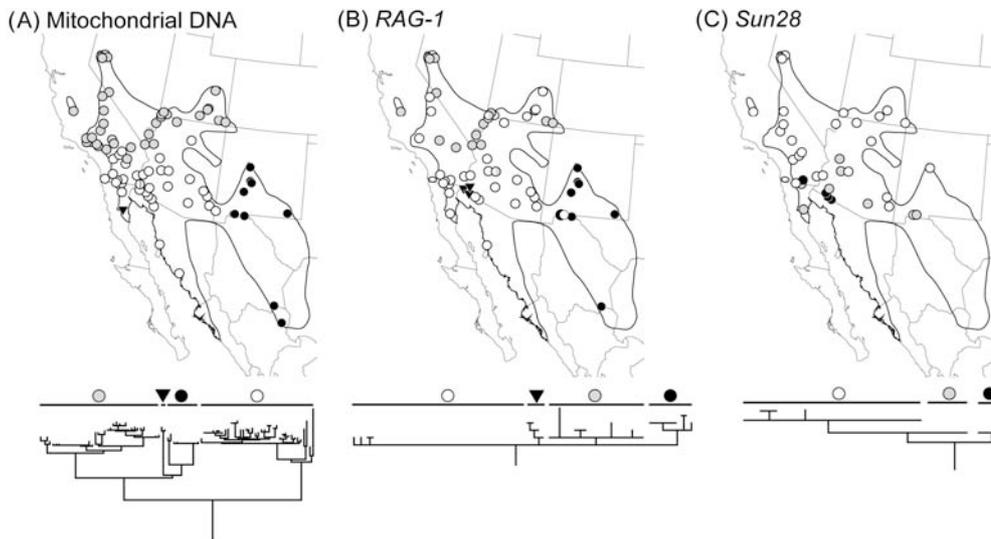


**Fig. 4** Phylogenetic relationships within the *Sceloporus magister* species group based on a partitioned Bayesian analysis of mtDNA data (1606bp). Divergence dates are provided for the nodes identified by letters in Table 2. The pre-existing names for the major clades within *S. magister* are designated, although a new basal lineage adds a fourth clade (unnamed) to the *S. magister* mtDNA genealogy. Haplotypes sampled from Yuma, Yuma Co., AZ (Locality 29; connected by arrows) group with *S. 'uniformis'* and *S. 'magister'*, which disrupts the exclusivity of these putative species.

*Relaxed phylogenetic analysis*

Posterior estimates of divergence times under the uniform, normal and log-normal prior distributions on the root node are provided in Table 2. The uniform and log-normal priors result in posterior mean ages and 95% HPD estimates that are older relative to the normal distribution. This pattern is

not surprising, since our implementations of the uniform and log-normal distributions allowed broader searches of parameter space compared to the more restrictive normal distribution, which also focused prior density on ages postdating the first appearance of *Sceloporus* in the fossil record. The log-normal prior produced younger posterior mean ages compared to the uniform distribution, and the



**Fig. 5** Intraspecific genealogies and area cladograms for *Sceloporus magister* based on a partitioned Bayesian analysis of the mtDNA data and maximum likelihood analyses of the nuclear loci. The mtDNA genealogy (A) strongly supports four major phylogeographical partitions, although two of these phylogroups are rendered non-exclusive by the overlap of haplotypes at Yuma, AZ (Locality 29). The low levels of sequence variation in the nuclear genes (B and C) do not provide strong support for any phylogeographical subdivisions, although the *RAG-1* genotypes provide weak signal for a phylogroup associated with the Chihuahuah Desert (B). The *BDNF* and *sun32* loci are not shown.

95% HPD estimates under the uniform distribution are broader (Table 2). These patterns verify that the uniform and log-normal priors are allowing broad explorations of parameter space, but that the log-normal distribution is in fact placing higher prior-density closer to the observed fossil age at 25 Ma.

A chronology of divergence times for the *magister* group based on the log-normal prior distribution results in high mean posterior density for more recent divergence events in the group, while the oldest divergence times are accompanied by broad 95% HPD estimates (Fig. 6; Table 2). The narrow HPD estimates accompanying recent divergence events are an artefact of the analysis not being able to sample divergence times younger than 0.0 million years (my). The posterior mean estimate for the age of the *magister* group is 6.481 Ma with a broad 95% HPD (Table 2). The mean separation of *S. magister* and *S. zosteromus* is ca. 1.3 my earlier than the initial divergence event in the *S. orcutti* complex (Fig. 6). Diversification within *S. magister* began 3.4 Ma, which is ca. 0.75 my earlier than the speciation event within the *orcutti* complex that separated *S. orcutti* and *S. hunsakeri* (Fig. 6). The division of *S. zosteromus* into northern and southern clades on the Baja California Peninsula occurred at approximately the same time (2.97 Ma; Fig. 6). Within *S. magister*, diversification within the Sonoran Desert clade predates the Chihuahuan and Mojave Desert clades by 0.7 my (Fig. 6). The posterior mean age estimate for the divergence of *S. zosteromus* on Isla Monserrate is 1.57 Ma (Table 2), which is 0.43 my earlier than the prior mean age that we implemented in our divergence dating analysis.

#### Gene-flow estimates

The geometric mean of the gene mutation rates for the four nuclear loci, corrected for generation time, was  $4.92466 \times 10^{-6}$  ( $RAG-1 = 2.75604 \times 10^{-6}$ ;  $BDNF = 1.4764 \times 10^{-6}$ ;  $Sun27 = 3.49701 \times 10^{-6}$ ;  $Sun32 = 2.11987 \times 10^{-6}$ ). The marginal posterior probabilities for the migration-rate parameters reveal strong asymmetrical migration between sub-populations of *S. magister* (Table 3). Interestingly, the asymmetry in migration rates suggests that gene flow into the *magister* mtDNA clade from the *uniformis* and *bimaculosus* clades is much more prevalent compared to the reverse direction (Table 3). The ML estimates for the population migration rates (the effective rate of genes entering a population, per generation) for gene flow into the *magister* clade from *bimaculosus* and *uniformis* are 9.92 (90% HPD interval: 0.025, 39.161) and 18.78 (90% HPD interval: 6.897, 60.467), respectively (Table 3). The ML estimates for divergence times suggest that *magister* and *uniformis* diverged more recently than did *magister* and *bimaculosus* (2.0 vs. 4.3 Ma; Table 3). Estimates of effective population sizes vary over an order of magnitude in most cases, and the ancestral effective population size estimates vary by up to three orders of magnitude (Table 3).

#### Ancestral area reconstructions

The Sonoran Desert is the ancestral area for *S. magister*, and expansions into all other areas are supported, excluding the Great Basin, which was reached via the Mojave Desert

**Table 2** Divergence times for clades in the *Sceloporus magister* species group based on a relaxed phylogenetic analysis of mtDNA data. Posterior mean ages (Ma) are provided for analyses conducted under uniform, normal, and log-normal prior distributions on the root age

Clade	Root Prior	Posterior mean age (95% HPD)	SD	ESS
A) <i>magister</i> group	uniform	8.315 (1.96, 15.767)	0.159	550
	normal	6.227 (0.987, 13.424)	0.336	120
	lognormal	6.481 (0.918, 12.358)	0.152	419
B) <i>orcutti</i> complex	uniform	5.735 (1.291, 11.11)	0.122	479
	normal	4.108 (0.575, 8.694)	0.165	212
C) <i>magister</i> complex	lognormal	4.226 (0.602, 8.193)	0.101	431
	uniform	7.16 (1.592, 13.563)	0.138	549
	normal	5.227 (0.892, 10.95)	0.256	135
D) <i>S. orcutti</i> + <i>S. hunsakeri</i>	lognormal	5.569 (1.004, 10.843)	0.134	406
	uniform	3.621 (0.769, 6.997)	0.07703	506
	normal	2.522 (0.418, 5.288)	0.0906	256
E) <i>S. zosteromus</i>	lognormal	2.652 (0.369, 5.171)	0.0624	463
	uniform	3.901 (0.829, 7.429)	0.07432	586
	normal	2.782 (0.478, 5.702)	0.09808	244
F) <i>S. zosteromus</i> : Isla Monserrate	lognormal	2.977 (0.446, 5.626)	0.06256	521
	uniform	1.99 (0.578, 3.483)	0.02356	1077
	normal	1.469 (0.238, 2.856)	0.03719	379
G) <i>S. magister</i>	lognormal	1.574 (0.254, 2.877)	0.02716	673
	uniform	4.483 (1.126, 8.534)	0.08683	554
	normal	3.228 (0.53, 6.703)	0.158	137
H) <i>S. magister</i> : Sonora	lognormal	3.393 (0.582, 6.359)	0.06623	579
	uniform	2.755 (0.654, 5.331)	0.05279	601
	normal	1.986 (0.356, 4.224)	0.07427	239
I) <i>S. magister</i> : Chihuahua + Mojave + N. Baja	lognormal	2.062 (0.419, 4.056)	0.04036	633
	uniform	3.229 (0.785, 6.241)	0.06669	510
	normal	2.289 (0.398, 4.802)	0.08605	236
J) <i>S. magister</i> : Mojave	lognormal	2.406 (0.396, 4.587)	0.05299	479
	uniform	1.753 (0.402, 3.402)	0.0332	640
	normal	1.266 (0.189, 2.766)	0.05	245
K) <i>S. magister</i> : Chihuahua	lognormal	1.307 (0.259, 2.553)	0.02756	541
	uniform	1.807 (0.331, 3.615)	0.03252	855
	normal	1.267 (0.13, 2.808)	0.0577	276
	lognormal	1.332 (0.146, 2.735)	0.02841	674

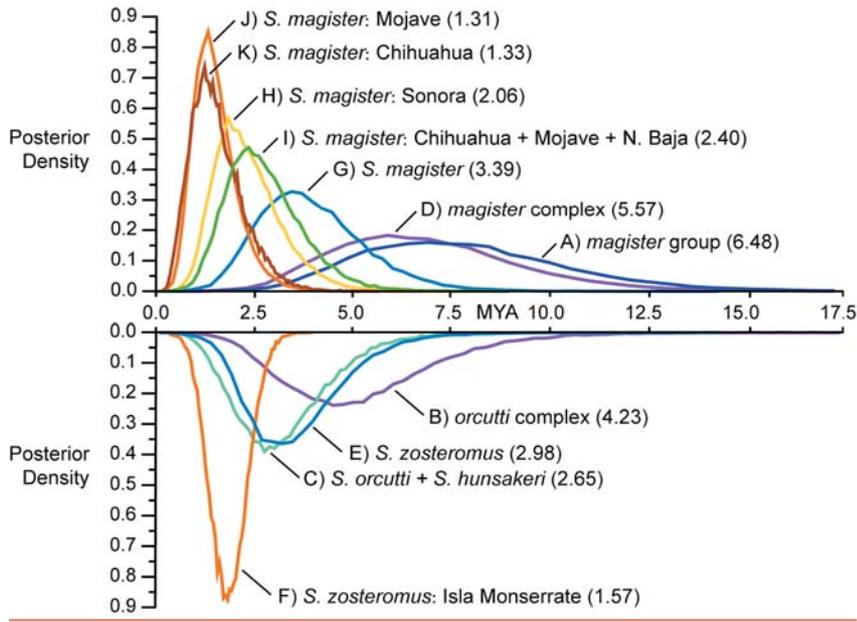
(Fig. 7). Alternative parsimony reconstructions using DELTRAN and ACCTRAN optimizations support an identical number of events involving the Sonoran Desert, but the number and direction of events involving the Mojave Desert, Great Basin and NACR differs, particularly by the addition of an event from the Great Basin to the NACR (Fig. 7). The Colorado Plateau and NACR include both Mojave and Sonoran Desert components (Fig. 7).

## Discussion

### *Biogeography and diversification of the peninsular endemics*

The palaeogeographical history of the Baja California Peninsula is incredibly dynamic, and it is well established that the Baja California Peninsula separated from mainland

Mexico as the peninsula was transferred from the North American Plate to the Pacific Plate along the San Andreas Fault (Carreño & Helenes 2002). This geological event occurred in two major phases, beginning with the initial separation of the Cape Region in the middle to late Miocene (Stock & Hodges 1989; Ferrari 1995; Lee *et al.* 1996), followed by the northern peninsula rifting from a more northern region (Holt *et al.* 2000; Carreño & Helenes 2002). Our phylogenetic analyses support a history involving sequential divergence events on the Baja California Peninsula, and our divergence dating analyses confirm that the origination of the peninsular endemics in the *Sceloporus magister* group are coincident with the timing of these geological events. The most recent common ancestor of the *orcutti* complex rifted from the mainland on the Cape Region and was followed closely by the isolation of *S. zosteromus* on the northern peninsula. Parallel divergences in the form



**Fig. 6** Chronology of divergence times for the major clades in the *Sceloporus magister* species group based on a relaxed phylogenetic analysis of mtDNA and a log-normal prior distribution for the root age of *Sceloporus*. Posterior distributions for the *orcutti* complex and *S. zosteromus* are shown below the x-axis.

of two sequential divergence events resulting from the initial formation of the Baja California Peninsula have not been proposed for any other taxonomic group, as far as we are aware. This biogeographical scenario has remained undetected in this group because previous studies did not realize the sister taxon relationship between the *orcutti* and *magister* complexes (see section on systematics below).

The Cape and northern portions of the emergent Baja California Peninsula were eventually joined, but fluctuating sea levels severed the connection multiple times and provided opportunities for further diversification (Riddle *et al.* 2000; Murphy & Aguirre-Leon 2002). The third divergence event in the *magister* species group occurred during the early Pliocene (4.2 Ma; Fig. 6) and separated the Cape endemic *S. licki* from the most recent common ancestor of *S. orcutti* and *S. hunsakeri* (Figs 3, 4 and 6). Interestingly, the Cape Region was reinvaded approximately 1.6 my later during the late Pliocene (2.65 Ma), resulting in two *S. orcutti* complex members restricted to the Cape Region, *S. licki* and *S. hunsakeri*. The occurrence of *S. orcutti* on the Isla Tortuga in the Gulf of California (Murphy & Aguirre-Leon 2002), a deep-water island that was probably never connected to the peninsula, suggests that a reinvasion of the Cape Region from the northern peninsula via overwater dispersal is plausible.

Coincident phylogeographical divergences in mtDNA genealogies are recorded at the mid-peninsula of Baja California in a variety of co-distributed species (Lindell *et al.* 2006). A seaway spanning the mid-peninsula is most often invoked as the vicariant event responsible for producing

these shared genealogical patterns (Upton & Murphy 1997; Riddle *et al.* 2000), but this hypothesis is controversial because of a lack of any geological evidence (Crews & Hedin 2006). In addition, a recent study examining the timing of population divergences across multiple taxon pairs separated at the mid-peninsula rejected the single-seaway hypothesis and suggested that more than one event is responsible for structuring genetic diversity in Baja California (Leaché *et al.* in press). This region appears to be a genetic barrier in *S. zosteromus* as indicated by the basal divergence we recovered within this species (Fig. 4); however, further sampling is required to localize the boundary between the northern and southern clades. We estimated the date of this divergence to the late Pliocene (2.97 Ma; Table 2). We found no evidence of a mid-peninsular divergence in *S. orcutti* (Fig. 4), even though our sampling included individuals from San Ignacio and Santa Agueda (just east of Santa Rosalia), which are located on both sides of the putative seaway.

Given the same amount of evolutionary time to diverge, *S. zosteromus* appears to have remained one geographically variable species on the Baja California Peninsula, presumably connected by gene flow, while the common ancestor of the *orcutti* complex has produced three species that are apparently reproductively isolated. These dissimilar patterns of geographical variation and speciation may be linked to ecological and behavioural preferences. *S. orcutti* and *S. hunsakeri* typically utilize large rocky outcrops, whereas *S. licki* is more often found in arboreal habitats associated with rocks and logs near low trees (Hall & Smith 1979; Grismer 2002). Thus, the *orcutti*–*hunsakeri* ancestor

	<i>S. magister</i> + <i>S. bimaculosus</i>		<i>S. magister</i> + <i>S. uniformis</i>	
	MLE	90% HPD	MLE	90% HPD
$\theta_1$	0.3721	0.1691/1.3867	11.2132	6.2418/24.1387
$\theta_2$	9.7748	5.1073/20.6658	1.3809	0.7549/2.1911
$\theta_A$	0.5881	0.0507/101.4179	12.2074	0.0552/110.4193
$t$	10.575	3.285/20.115	4.99	1.79/7.89
$m1$	0.19	0.01/2.29	3.35	2.21/5.01
$m2$	2.03	0.01/3.79	0.005	0.005/0.545
$N_1$	18 890	8 584/70 396	569 237	316 865/1 225 400
$N_2$	496 217	259 272/1 049 098	70 101	38 322/111 231
$N_A$	29 855	2 574/5 148 473	619 708	2 802/5 605 429
$t$	4 294 713	1 334 102/8 169 093	2 026 536	726 954/3 204 283
$m1$ ( <i>mag.</i> → <i>x</i> )	0.04	0.00/ 1.59	18.78	6.90/60.47
$m2$ ( <i>x</i> → <i>mag.</i> )	9.92	0.03/ 39.16	0.00	0.00/0.60

**Table 3** Population genetic model parameter estimates and scaled demographic values for comparisons between the *Sceloporus magister* + *S. bimaculosus* and *S. magister* + *S. uniformis* mtDNA clades. The maximum likelihood estimate (MLE) is equivalent to the peak of the marginal posterior probability distribution. HPD, highest posterior density

may have successfully reinvaded the Cape Region because of ecological and behavioural differences with respect to the Cape resident, *S. licki*. Upon reconnection of the Cape Region and the northern Peninsula, *S. orcutti* and *S. hunsakeri* may have remained isolated because the appropriate intervening rocky habitat was missing, which is apparent today as a distributional gap at the Isthmus of La Paz (Grismer 2002). However, we note that these ecological differences may be oversimplifications and that each of these species has been observed on a broader range of habitat types (Grismer 2002). The distribution of *S. zosteromus* is continuous along the peninsula, and three distinctive subspecies that appear to intergrade widely are recognized (Grismer 2002). This is in contrast to *S. orcutti*, which occurs from just north of the Cape Region to Southern California and shows very little geographical variation in morphology. The divergence of *S. zosteromus* in the Cape Region (*S. z. zosteromus*), may have occurred in parallel with diversification in the *orcutti* complex; however, the ability of *S. zosteromus* to occupy a wide range of habitats, including rocky outcrops, brush thicket, sandy flats and dune habitat (Grismer 2002), may have permitted secondary contact and gene flow between *S. zosteromus* populations upon reconnection of the Cape Region and the northern Peninsula.

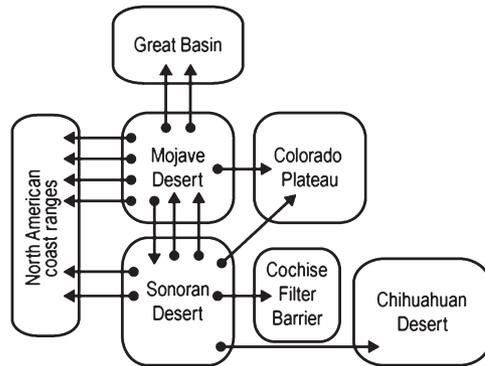
#### Continental phylogeography in *Sceloporus magister*

Our broad geographical sampling of *S. magister* provides new insights into the biogeography of the arid deserts. One interesting result is the polyphyly of samples of *S. m. 'cephaloflavus'* from the Colorado Plateau. Previous phylogeographical analyses only included samples from the southern portion of the Colorado Plateau and concluded

that all Colorado Plateau populations originated from the Sonoran Desert (Orange 1997; Schulte *et al.* 2006). Interestingly, Tanner (1955) remarked that populations of *S. magister* in the southern Colorado Plateau (including northern Arizona and southwestern Utah) were morphological intermediates between '*uniformis*' and '*cephaloflavus*' and suggested that this area represents a wide intergrade zone. Indeed, our samples from the southern portion of the Colorado Plateau (including Wupatki, AZ) are more closely related to Sonoran Desert populations than to other Colorado Plateau populations (Figs 4 and 5A; Orange 1997; Schulte *et al.* 2006). However, our samples from the northern portion of the Colorado Plateau are nested within a Mojave Desert clade that also includes samples from the Great Basin. This pattern is seen in other groups such as night lizards (*Xantusia*; Sinclair *et al.* 2004), night snakes (*Hypsiglena*; Mulcahy 2006) and rattlesnakes (*Crotalus*; Pook *et al.* 2000; Ashton & de Queiroz 2001). The mixed ancestry of the Colorado Plateau is illustrated in our ancestral area reconstructions (Fig. 7).

Another unique area relationship supported by our mtDNA genealogy pertains to the placement of the Chihuahuan Desert clade sister to the Mojave Desert and northern Baja California clades (Figs 4 and 5A). Previous phylogeography studies of vertebrates in this region have recovered the Chihuahuan Desert as either the most basal (Upton & Murphy 1997; Mulcahy 2006), sister to the Sonoran Desert (Riddle *et al.* 2000; Devitt 2006; Riddle & Hafner 2006) or sister to the Colorado Plateau (Jaeger *et al.* 2005). Biogeographically, this novel area relationship is difficult to explain without assuming that the Colorado Plateau provided a link between the Mojave and Chihuahuan Desert populations. This scenario is not supported by our

## (A) Delayed transformation



## (B) Accelerated transformation

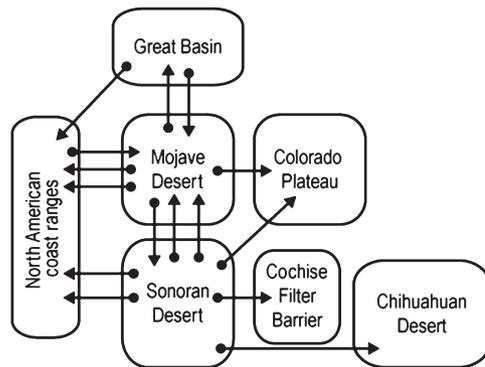


Fig. 7 Historical biogeography of *Sceloporus magister* based on parsimony reconstructions of ancestral areas on the mtDNA genealogy optimized using (A) delayed transformation (DELTRAN) and (B) accelerated transformation (ACCTRAN). The Sonoran Desert is the ancestral area for *S. magister*, and arrows indicate unambiguous relationships among areas.

parsimony reconstructions, which support an unambiguous transformation between the Sonoran and Chihuahuan Deserts (Fig. 7). One possible explanation for the atypical placement of the Chihuahuan Desert clade is that the mtDNA genealogy is suffering from lineage sorting problems. Our nuclear *RAG-1* data suggest that the Chihuahuan Desert population is distinct (albeit weakly supported; Fig. 5b), but gene flow connects the Chihuahuan and Sonoran Desert populations of *S. magister* (Table 3). More importantly, nuclear estimates for the time of population splitting parameter ( $t$ ) obtained from our Isolation with Migration analyses indicate that the population split between the *magister* (Sonoran Desert) + *bimaculosus* (Chihuahuan Desert) clades occurred earlier than the *magister* (Sonoran Desert) + *uniformis* (Mojave and Great Basin Deserts) clades (Table 3). Thus, our nuclear data, although limited in variability, suggest that the history of population separation in *S. magister* conforms to a more traditional biogeographical pattern.

*Systematics of the Sceloporus magister species group*

*S. lineatulus* on Isla Santa Catalina was originally described as a distinct species (Dickerson 1919), although later systematic work on the *magister* complex treated it as a subspecies of *S. magister* (Phelan & Brattstrom 1955; Tanner 1955; Parker 1982). Most recent studies recognize the unique evolutionary history of the island population and refer to it as *S. lineatulus* (Murphy 1983a, b; Grismer & McGuire 1996; Wiens & Reeder 1997). Our phylogenetic analyses provide the first evidence for *S. zosteromus* paraphyly with respect to *S. lineatulus* (Fig. 4), although our sampling of *S. lineatulus* included only one small fragment of the 12S rRNA gene taken from GenBank (Wiens & Reeder 1997). Based on adult male colour patterns, Phelan & Brattstrom (1955) believed that *S. lineatulus* was most closely related to *S. z. zosteromus* on the Cape Region, although our phylogenetic analysis (Fig. 4) places *S. lineatulus* within a clade containing *S. z. monserratisensis* and *S. z. zosteromus*. In cases involving recent island colonization from the mainland, such as the situation presented by *S. lineatulus*, monophyly is a difficult species criterion to satisfy since it renders the ancestral mainland population paraphyletic (de Queiroz & Donoghue 1988; Hudson & Coyne 2002). We recommend the continued recognition of *S. lineatulus* and *S. zosteromus* and suggest that future studies of species limits in this group focus on the evolutionary processes occurring between the major clades that we have identified on the Baja California Peninsula.

Phelan & Brattstrom (1955) suggested that *S. magister* is at an early stage of regional and ecological specialization because the only phenotypic differences separating subspecies are adult male colour patterns. However, genetic diversification within *S. magister* actually began in the Late Pliocene (3.39 Ma; Table 2), which implies that the corresponding evolution of discrete phenotypes between populations could have been impeded by gene flow. However, delimiting taxa within *S. magister* using colour pattern characters presents some challenges. First, the geographical limits of the subspecies proposed by Phelan & Brattstrom (1955) are imprecise and based on the examination of a limited amount of material. Parker (1982) was the first to note this problem and called for a re-evaluation of morphological variation. For instance, Phelan & Brattstrom (1955) depicted the distribution of *S. m. bimaculosus* extending far into eastern Arizona; however, the only two individuals they examined from Arizona were deemed intergrades with '*S. m. magister*'. Second, colour patterns appear to be highly labile and a poor predictor of phylogenetic relationships in *Sceloporus* (Leaché & Reeder 2002; Wiens & Penkrot 2002), and *S. magister* appears to be no different as measured by subspecies polyphyly (Fig. 4). Last, wide zones of intergradation make it difficult to classify some populations (Phelan & Brattstrom 1955).

The major mtDNA clades within *S. magister* help illuminate the biogeographical history of western North American deserts, but they do not necessarily represent independent evolutionary lineages that warrant species recognition. Genealogical exclusivity is violated by the mtDNA data, and this problem spans the root of the *S. magister* genealogy (Fig. 4). The population with admixed mtDNA haplotypes is located in Yuma, AZ, near the type locality of *S. magister*; more importantly, it is situated near the centre of the range of one of the major mtDNA clades. This geographical pattern of admixture suggests that these clades overlap over a considerable distance along the Colorado River, although our sampling in this area is too sparse to resolve the distribution of these clades in fine detail. If the admixed population was located at the boundary of two clades, then one could argue that a narrow zone of hybridization and/or mtDNA introgression was the cause for a lack of exclusivity. Given that we rarely sequenced more than one individual from any given locality, we predict that increased sampling within populations will only provide more examples of genetic admixture in *S. magister*. In addition, the Isolation with Migration analyses of the nuclear loci indicate that barriers to gene flow do not exist between the mtDNA clades. Despite temporary periods of geographical isolation and genetic and phenotypic diversification, these data suggest that recognizing multiple species within *S. magister* is not warranted, and that nuclear gene flow has continued to prevent speciation in *S. magister*. We recommend the continued recognition of *S. magister* as a single species and anticipate that future studies utilizing more variable nuclear loci will provide greater details pertaining to the genetic landscape of *S. magister*.

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## References

- Arbogast BS, Edwards SV, Wakeley J, Beerli P, Slowinski JB (2002) Estimating divergence times from molecular data on phylogenetic and population genetic timescales. *Annual Review of Ecology and Systematics*, **33**, 707–740.
- Ashton KG, de Queiroz A (2001) Molecular systematics of the western rattlesnake, *Crotalus viridis* (viperidae), with comments on the utility of the D-loop in phylogenetic studies of snakes. *Molecular Phylogenetics and Evolution*, **21**, 176–189.
- Brandley MC, Schmitz A, Reeder TW (2005) Partitioned bayesian analyses, partition choice, and the phylogenetic relationships of scincid lizards. *Systematic Biology*, **54**, 373–390.
- Brattstrom BH (1953) Records of Pleistocene reptiles from California. *Copeia*, 174–179.
- Carreño AL, Helenes J (2002) Geology and ages of the islands. In: *A New Island Biogeography of the Sea of Cortés* (eds Case TJ, Cody ML, Ezcurra E), pp. 14–40. Oxford University Press, Oxford, UK.
- Cole CJ, Van Devender TR (1976) Surface structure of fossil and recent epidermal scales from North American lizards of the genus *Sceloporus* (reptilia, iguanidae). *Bulletin of the American Museum of Natural History*, **156**, 451–514.
- Crews SC, Hedin M (2006) Studies of morphological and molecular phylogenetic divergence in spiders (araneae: *homalonychus*) from the American southwest, including divergence along the Baja California Peninsula. *Molecular Phylogenetics and Evolution*, **38**, 470–487.
- Devitt TJ (2006) Phylogeography of the western lyresnake (*Trimorphodon biscutatus*): testing aridland biogeographical hypotheses across the Nearctic-Neotropical transition. *Molecular Ecology*, **15**, 4387–4407.
- Dickerson MC (1919) Diagnosis of twenty-three new species and a genus of lizards from Lower California. *Bulletin of the American Museum of Natural History*, **41**, 461–477.
- Drummond AJ, Rambaut A (2006) BEAST version 1.4, Available from <http://beast.bio.ed.ac.uk/>.
- Drummond AJ, Ho SYW, Phillips MJ, Rambaut A (2006) Relaxed phylogenetics and dating with confidence. *PLoS Biology*, **4**, e88.
- Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, **32**, 1792–1797.
- Ferrari L (1995) Miocene shearing along the northern boundary of the Jalisco block and the opening of the southern Gulf of California. *Geology*, **23**, 751–754.
- Flores-Villela O, Kjer KM, Benabib M, Sites JW Jr (2000) Multiple data sets, congruence, and hypothesis testing for the phylogeny of basal groups of the lizard genus *Sceloporus* (squamata, phrynosomatidae). *Systematic Biology*, **49**, 713–739.
- Gastil G, Minch J, Phillips RP (1983) The geology and ages of islands. In: *Island Biogeography in the Sea of Cortés* (eds Case TJ, Cody ML), pp. 13–15. California University Press, Berkeley, CA.
- Grismer LL (1994) The origin and evolution of the peninsular herpetofauna of Baja California, Mexico. *Herpetological Natural History*, **2**, 51–106.
- Grismer LL (2002) *Amphibians and Reptiles of Baja California Including its Pacific Islands and the Islands in the Sea of Cortes*. University of California Press, Berkeley, CA.
- Grismer LL, McGuire JA (1996) Taxonomy and biogeography of the *Sceloporus magister* complex (squamata: phrynosomatidae) in Baja California, Mexico. *Herpetologica*, **52**, 416–427.
- Hall WP, Smith HM (1979) Lizards of the *Sceloporus orcutti* complex of the Cape Region of Baja California. *Breviora*, **452**, 1–26.

- Hasegawa M, Kishino H, Yano TA (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, **22**, 160–174.
- Hey J, Nielsen R (2004) Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*. *Genetics*, **167**, 747–760.
- Ho SYW (2007) Calibrating molecular estimates of substitution rates and divergence times in birds. *Journal of Avian Biology*, **38**, 409–414.
- Holman JA (1970) A Pleistocene herpetofauna from Eddy County, New Mexico. *Texas Journal of Science*, **22**, 29–39.
- Holman JA (1995) *Pleistocene Amphibians and Reptiles of North America*. Oxford University Press, New York.
- Holt JW, Holt EW, Stock JM (2000) An age constraint on Gulf of California rifting from the Santa Rosalia Basin, Baja California Sur, Mexico. *Geological Society of America Bulletin*, **112**, 540–549.
- Hudson RR, Coyne JA (2002) Mathematical consequences of the genealogical species concept. *Evolution*, **56**, 1557–1565.
- Hudson RR, Turelli M (2003) Stochasticity overrules the ‘three-times rule’: Genetic drift, genetic draft, and coalescent times for nuclear loci versus mitochondrial DNA. *Evolution*, **57**, 182–190.
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, **17**, 754–755.
- Jaeger JR, Riddle BR, Bradford DF (2005) Cryptic Neogene vicariance and Quaternary dispersal of the red-spotted toad (*Bufo punctatus*): insights on the evolution of North American warm desert biotas. *Molecular Ecology*, **14**, 3033–3048.
- Leaché AD, McGuire JA (2006) Phylogenetic relationships of horned lizards (*Phrynosoma*) based on nuclear and mitochondrial data: evidence for a misleading mitochondrial gene tree. *Molecular Phylogenetics and Evolution*, **39**, 628–644.
- Leaché AD, Reeder TW (2002) Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. *Systematic Biology*, **51**, 44–68.
- Leaché AD, Crews SC, Hickerson MJ (2007) Two waves of diversification in mammals and reptiles of Baja California revealed by hierarchical Bayesian analysis. *Biology Letters*, doi: 10.1098/rsbl.2007.0368.
- Lee J, Miller MM, Crippen R, Hacker B, Vazquez JL (1996) Middle Miocene extension in the Gulf Extensional Province, Baja California; evidence from the southern Sierra Juarez. *Geological Society of America Bulletin*, **108**, 505–525.
- Lindell J, Ngo A, Murphy RW (2006) Deep genealogies and the mid-peninsular seaway of Baja California. *Journal of Biogeography*, **33**, 1327–1331.
- Maddison DR, Maddison WP (2000) *MacClade 4: Analysis of Phylogeny and Character Evolution*. Sinauer Associates, Sunderland, MA.
- Moore WS (1995) Inferring phylogenies from mtDNA variation: Mitochondrial-gene trees versus nuclear-gene trees. *Evolution*, **49**, 718–726.
- Mulcahy DG (2006) Historical biogeography of North American nightsnakes and their relationships among the dipsadines: evidence for vicariance associated with Miocene formations of North-western Mexico. PhD thesis, Utah State University, Logan, UT.
- Murphy RW (1983a) Paleobiogeography and genetic differentiation of the Baja California herpetofauna. *Occasional Papers of the California Academy of Sciences*, **137**, 1–48.
- Murphy RW (1983b) The reptiles: origins and evolution. In: *Island Biogeography in the Sea of Cortés* (eds Case TJ, Cody ML), pp. 130–158. University of California Press, Berkeley, CA.
- Murphy RW, Aguirre-Leon G (2002) The nonavian reptiles: origins and evolution. In: *A New Island Biogeography of the Sea of Cortés* (eds Case TJ, Cody ML, Ezcurra E), pp. 181–220. Oxford University Press, Oxford.
- Nylander JAA (2004) MRMODELTEST, Version 2. Evolutionary Biology Centre, Uppsala University, Uppsala.
- Orange DI (1997) Comparative biogeography within and among four species of lizards in western North American deserts. PhD thesis, University of Nevada, Reno, NV.
- Parker WS (1982) *Sceloporus magister*. *Catalog of American Amphibians and Reptiles*, **290**, 1–4.
- Parker WS, Pianka ER (1973) Notes on the ecology of the iguanid lizard, *Sceloporus magister*. *Herpetologica*, **29**, 143–152.
- Phelan RL, Brattstrom BH (1955) Geographic variation in *Sceloporus magister*. *Herpetologica*, **11**, 1–14.
- Pook CE, Wüster W, Thorpe RS (2000) Historical biogeography of the western rattlesnake (serpentes: viperidae: *Crotalus viridis*), inferred from mitochondrial DNA sequence information. *Molecular Phylogenetics and Evolution*, **15**, 269–282.
- de Queiroz K, Donoghue MJ (1988) Phylogenetic systematics and the species problem. *Cladistics*, **4**, 317–338.
- Rambaut A, Drummond AJ (2004) *TRACER*. University of Oxford, Oxford.
- Riddle BR, Hafner DJ (2006) A step-wise approach to integrating phylogeographic and phylogenetic biogeographic perspectives on the history of a core North American warm deserts biota. *Journal of Arid Environments*, **66**, 435–461.
- Riddle BR, Hafner DJ, Alexander LF, Jaeger JR (2000) Cryptic vicariance in the historical assembly of a Baja California Peninsular Desert biota. *Proceedings of the National Academy of Sciences, USA*, **97**, 14438–14443.
- Robinson MD, Van Devender TR (1973) Miocene lizards from Wyoming and Nebraska. *Copeia*, 698–704.
- Ronquist F, Huelsenbeck JP (2003) MRBAYES, Version 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**, 1572–1574.
- Rosenblum EB, Belfiore NM, Moritz C (2007) Anonymous nuclear markers for the eastern fence lizard, *Sceloporus undulatus*. *Molecular Ecology Notes*, **7**, 113–116.
- Rutschmann F (2006) Molecular dating of phylogenetic trees: a brief review of current methods that estimate divergence times. *Diversity Distrib*, **12**, 35–48.
- Savage JM (1960) Evolution of a peninsular herpetofauna. *Systematic Zoology*, **9**, 184–212.
- Schulte JA, Macey JR, Papenfuss TJ (2006) A genetic perspective on the geographic association of taxa among arid North American lizards of the *Sceloporus magister* (squamata: iguanidae: phrynosomatidae). *Molecular Phylogenetics and Evolution*, **39**, 873–880.
- Sinclair EA, Bezy RL, Bolles K *et al.* (2004) Testing species boundaries in an ancient species complex with deep phylogeographic history: genus *Xantusia* (squamata: xantusiidae). *American Naturalist*, **164**, 396–414.
- Sites Jr JW, Archie JW, Cole CJ, Vilella OF (1992) A review of phylogenetic hypotheses for lizards of the genus *Sceloporus* (phrynosomatidae): Implications for ecological and evolutionary studies. *Bulletin of the American Museum of Natural History*, **213**, 1–110.
- Stamatakis A (2006) RAXML-VI-HPC: maximum likelihood-based phylogenetic analysis with thousands of taxa and mixed models. *Bioinformatics*, **22**, 2688–2690.

- Stock JM, Hodges KV (1989) Pre-Pliocene extension around the Gulf of California and the transfer of Baja California to the Pacific Plate. *Tectonics*, **8**, 99–115.
- Tanner WW (1955) A new *Sceloporus magister* from eastern Utah. *Great Basin Naturalist*, **15**, 1–4.
- Thorne JL, Kishino H (2005) Estimation of divergence times from molecular sequence data. In: *Statistical Methods in Molecular Evolution* (ed. Nielsen R), pp. 233–256. Springer, New York.
- Upton DE, Murphy RW (1997) Phylogeny of the side-blotched lizards (phrynosomatidae: *Uta*) based on mtDNA sequences: Support for a midpeninsular seaway in Baja California. *Molecular Phylogenetics and Evolution*, **8**, 104–113.
- Welsh HHJ (1988) An ecogeographic analysis of the herpetofauna of the Sierra San Pedro Martir Region, Baja California, with a contribution to the biogeography of the Baja California herpetofauna. *Proceedings of the California Academy of Sciences 4th Series*, **46**, 1–72.
- Wiens JJ, Penkrot TA (2002) Delimiting species using DNA and morphological variation and discordant species limits in Spiny Lizards (*Sceloporus*). *Systematic Biology*, **51**, 69–91.
- Wiens JJ, Reeder TW (1997) Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. *Herpetological Monographs*, **11**, 1–101.
- Wilgenbusch JC, Warren DL, Swofford DL (2004) AWTY: A system for graphical exploration of MCMC convergence in Bayesian phylogenetic inference. <http://ceb.csit.fsu.edu/awty>.
- Won Y, Hey J (2005) Divergence population genetics of chimpanzees. *Molecular Biology and Evolution*, **22**, 297–307.
- Yang Z, Rannala B (2006) Bayesian estimation of species divergence times under a molecular clock using multiple fossil calibrations with soft bounds. *Molecular Biology and Evolution*, **23**, 212–226.
- Yatkola DA (1976) Mid-Miocene lizards from Western Nebraska. *Copeia*, 645–654.

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## Appendix I

Locality data and voucher specimen data for samples included in the study. Taxon ID numbers correspond to taxon labels in the phylogenetic trees and distribution maps. Region abbreviations are as follows: CFB, Cochise Filter Barrier; CHI, Chihuahuan Desert; CP, Colorado Plateau; GB, Great Basin Desert; MOJ, Mojave Desert; NACR, North American coast range; and SON, Sonoran Desert. Subspecies designations for *S. magister* include: bimac., *bimaculosus*; ceph., *cephaloflavus*; mag., *magister*; trans., *transversus*; uni., *uniformis*. Subspecies designations for *S. zosteromus* include: mon., *monserratisensis*; ruf., *rufidorsum*; and zost., *zosteromus*

Taxon ID	Locality	Region/ Subspecies	Voucher	mtDNA		Nuclear Loci			
				12S	ND4	BDNF	RAG-1	Sun27	Sun32
<i>Sceloporus hunsakeri</i>									
1a	Mexico: BCS; Los Barriles	SON	MVZ 236290	X	X	X	X		
1b	Mexico: BCS; Los Barriles	SON	MVZ 236291	X	X	X			
2	Mexico: BCS; El Triunfo	SON	RWM 619	X	X				
<i>Sceloporus licki</i>									
1	Mexico: BCS; Los Barriles	SON	MVZ 236292	X	X	X	X		
<i>Sceloporus lineatulus</i>									
1	Mexico: BCS; Santa Catalina Island	SON	GenBank:AF000810	X					
<i>Sceloporus magister</i>									
1	Mexico: BC; Laguna Salada	SON/uni.	DGM 486	X	X	X	X		
2a	Mexico: BC; Valle Santa Clara	SON/uni.	DGM 474	X	X	X	X	X	X
2b	Mexico: BC; Valle Santa Clara	SON/mag.	MVZ 236293	X	X	X	X		
3	Mexico: Chihuahua; Jimenez	CHI/bimac.	JRM 4860	X	X	X	X		
4	Mexico: Durango; Mapimi	CHI/bimac.	GAA 83-134		X				
5	Mexico: Sonora; El Desemboque	SON/mag.	MVZ 236298	X	X	X	X		
6	Mexico: Sonora; Guaymas	SON/mag.	GenBank:AF210345		X				
7	Mexico: Sonora; Sonoita	SON/mag.	ROM 14488	X	X				
8a	USA: AZ; Cochise Co., Bowie	CFB/bimac.	CAS 229188	X	X	X	X	X	X
8b	USA: AZ; Cochise Co., Bowie	CFB/bimac.	CAS 229156	X	X	X			
9	USA: AZ; Coconino Co., Wupatki	CP/uni.	CAS 229280		X			X	X
10	USA: AZ; Gila Co., Roosevelt	SON/bimac.	MVZ 232587	X	X	X	X		
11	USA: AZ; Graham Co., Emery	CFB/bimac.	CAS 229170	X	X	X	X		
12a	USA: AZ; Graham Co., Lebanon	CFB/bimac.	CAS 229159	X	X	X	X	X	X
12b	USA: AZ; Graham Co., Lebanon	CFB/bimac.	CAS 229160	X	X	X	X		
13	USA: AZ; La Paz Co., Quartzsite	SON/mag.	JAS294	X	X				
14	USA: AZ; La Paz Co., Yuma Proving Grounds	SON/mag.	CAS 229110	X	X	X	X	X	X
15	USA: AZ; Maricopa Co., Harquahala Mountains	SON/mag.	CAS 229150	X	X	X	X	X	X
16a	USA: AZ; Maricopa Co., Hassayampa River	SON/mag.	JRM 4401	X	X	X	X		
16b	USA: AZ; Maricopa Co., Hassayampa River	SON/mag.	JRM 4402	X	X	X	X	X	X
16c	USA: AZ; Maricopa Co., Hassayampa River	SON/mag.	JRM 4403	X	X	X	X		
17	USA: AZ; Maricopa Co., Maricopa Mountains	SON/mag.	CAS 229155	X	X	X			
18	USA: AZ; Mohave Co., Bulrush Wash	CP/uni.	CAS 229180	X	X	X		X	X
19	USA: AZ; Mohave Co., Burro Creek	SON/uni.	CAS 229084	X	X	X	X	X	X
20	USA: AZ; Mohave Co., Littlefield	MOJ/uni.	CAS 229080	X	X	X	X		
21	USA: AZ; Mohave Co., Stockton Hill Rd.	MOJ/uni.	CAS 229081	X	X	X	X		
22	USA: AZ; Mojave Co., Black Mountains	MOJ/uni.	JRM 4394	X	X	X	X		
23	USA: AZ; Pima Co., Tucson	SON/bimac.	KWS 238	X	X	X	X	X	X
24	USA: AZ; Yuma Co., Barry M. Goldwater AFR	SON/mag.	CAS 229096	X	X	X	X		
25	USA: AZ; Yuma Co., Cabeza Prieta N.W.R.	SON/mag.	CAS 229111	X	X	X	X	X	X
26	USA: AZ; Yuma Co., Pinacate Lava Flow	SON/mag.	CAS 229116	X	X	X	X	X	X
27	USA: AZ; Yuma Co., Copper Mountain	SON/mag.	CAS 229107	X	X	X	X	X	X
28	USA: AZ; Yuma Co., Mohawk Dunes	SON/mag.	CAS 229101	X	X	X	X	X	X
29a	USA: AZ; Yuma Co., Yuma	SON/mag.	JAS289	X	X				
29b	USA: AZ; Yuma Co., Yuma	SON/mag.	JAS290	X	X				
30	USA: CA; Fresno Co., Coalinga	NACR/uni.	MVZ 232697	X	X	X	X	X	X
31	USA: CA; Imperial Co., Coyote Mountains	SON/uni.	CAS 223600	X	X	X	X		
32	USA: CA; Imperial Co., Hwy 98	SON/uni.	CAS 229276	X	X	X	X	X	X
33	USA: CA; Imperial Co., Imler Rd.	SON/uni.	CAS 223530	X	X	X	X	X	X

Appendix I *Continued*

Taxon ID	Locality	Region/ Subspecies	Voucher	mtDNA		Nuclear Loci			
				12S	ND4	BDNF	RAG-1	Sun27	Sun32
34	USA: CA; Imperial Co., Midway Well	SON/uni.	CAS 223510	X	X	X	X	X	X
35a	USA: CA; Inyo Co., Alabama Hills	GB/trans.	CAS 214869	X	X	X	–	X	X
35b	USA: CA; Inyo Co., Alabama Hills	GB/trans.	CAS 214870	X	X	X	X	–	–
36	USA: CA; Inyo Co., Ninemile Canyon	MOJ/uni.	CAS 229029	X	X	–	X	X	X
37	USA: CA; Kern Co., Cottonwood Creek	NACR/uni.	MVZ 232622	X	X	X	X	–	–
38	USA: CA; Kern Co., Dove Springs	MOJ/uni.	DS2SP7-92	X	X	–	–	X	X
39	USA: CA; Los Angeles Co., Hungry Valley	NACR/uni.	DAW 0220	X	X	–	–	–	–
40	USA: CA; Los Angeles Co., Pearblossom	NACR/uni.	78-323	X	X	–	–	–	–
41	USA: CA; Los Angeles Co., Pearland	NACR/uni.	ROM 14610	X	X	–	–	–	–
42	USA: CA; Los Angeles Co., Piru Creek	NACR/uni.	ROM 23289	X	–	–	–	–	–
43	USA: CA; Mono Co., Pleasant Valley	GB/trans.	JQR 132	X	X	X	X	–	–
44	USA: CA; Riverside Co., Joshua Tree N.P.	MOJ/uni.	JOS 138	X	X	–	–	–	–
45	USA: CA; Riverside Co., Mesa	NACR/uni.	MES 441	–	X	–	–	X	X
46	USA: CA; San Bernardino Co., Burns Reserve	MOJ/uni.	BUR 167	–	X	–	–	X	X
47	USA: CA; San Bernardino Co., Daggett	MOJ/uni.	MVZ 150079	X	X	–	X	–	–
48	USA: CA; San Bernardino Co., Dale Dry Lake	MOJ/uni.	ROM 19838	X	X	–	–	–	–
49	USA: CA; San Bernardino Co., Granite Mountains	MOJ/uni.	DGMCF	X	X	–	X	–	–
50	USA: CA; San Bernardino Co., Hesperia	MOJ/uni.	MVZ 150080	X	X	–	–	–	–
51	USA: CA; San Bernardino Co., Marine Corp Center	MOJ/uni.	MCC	X	X	–	–	X	X
52	USA: CA; San Bernardino Co., Owl Canyon	MOJ/uni.	MVZ 179886	X	X	X	X	X	X
53	USA: CA; San Diego Co., Old Hwy 80	SON/uni.	CAS 223618	X	X	X	X	X	X
54	USA: CA; San Diego Co., San Diego N.W.R.	NACR/uni.	SWT 701	X	X	–	–	–	–
55	USA: CA; San Diego Co., San Felipe Valley	SON/uni.	CAS 223597	X	X	X	X	–	–
56	USA: NM; Dona Ana Co., Hwy A14	CHI/bimac.	TWR 230	X	X	X	X	–	–
57	USA: NM; Eddy Co., Pecos River	CHI/bimac.	CAS 229222	X	X	X	X	–	–
58	USA: NM; Hidalgo Co., Portal Road	CFB/bimac.	LSU 48819	X	–	–	–	–	–
59	USA: NM; Luna Co., CR 15	CHI/bimac.	CAS 229136	X	X	X	–	X	X
60	USA: NM; Luna Co., SSR 495	CHI/bimac.	CAS 229135	X	X	X	X	X	X
61	USA: NM; Sierra Co., Monticello Point	CHI/bimac.	DGM 891	X	X	X	X	–	–
62a	USA: NM; Socorro Co., Busqueido Rd.	CHI/bimac.	DGM 904	X	X	X	X	–	–
62b	USA: NM; Socorro Co., Busqueido Rd.	CHI/bimac.	DGM 905	X	X	X	X	–	–
63	USA: NM; Socorro Co., Hwy 380	CHI/bimac.	DGM 900	X	X	X	X	–	–
64	USA: NM; Valencia Co., Rio Puerco	CHI/bimac.	DGM 924	X	X	X	X	X	X
65	USA: NV; Churchill Co., Fallon	GB/uni.	MVZ 162077	X	X	X	X	–	–
66	USA: NV; Churchill Co., Hot Springs Flat	GB/uni.	CAS 223556	X	X	X	X	X	X
67	USA: NV; Clark Co., Hiko Springs	MOJ/uni.	CAS 223591	X	X	X	X	–	–
68	USA: NV; Clark Co., Virgin Mountains	MOJ/uni.	CAS 223375	X	X	X	X	X	X
69	USA: NV; Esmeralda Co., Fish Lake Valley	GB/trans.	CAS 229066	X	X	X	X	–	–
70	USA: NV; Lyon Co., Fernley	GB/uni.	CAS 223554	X	X	X	X	X	X
71	USA: NV; Washoe Co., Wadsworth	GB/uni.	CAS 223552	X	X	X	X	X	X
72	USA: UT; Emery Co., Saleratus Wash	CP/ceph.	CAS 229190	X	X	X	X	–	–
73	USA: UT; Garfield Co., Maidenwater Spring	CP/ceph.	CAS 229040	X	X	X	X	–	–
74a	USA: UT; Garfield Co., Star Creek	CP/ceph.	CAS 229057	X	X	–	X	–	–
74b	USA: UT; Garfield Co., Star Creek	CP/ceph.	CAS 229048	X	X	X	X	X	X
75	USA: UT; Kane Co., Hole-in-the-Rock	CP/ceph.	CAS 229173	X	X	X	X	X	X
76a	USA: UT; San Juan Co., Comb Wash	CP/ceph.	CAS 229178	X	X	X	X	–	–
76b	USA: UT; San Juan Co., Comb Wash	CP/ceph.	CAS 229179	X	X	X	X	–	–
77	USA: UT; San Juan Co., McElmo Creek	CP/ceph.	MVZ 235869	X	X	X	X	X	X
78a	USA: UT; Washington Co., Beaver Dam Slope	MOJ/uni.	MVZ 235866	X	X	X	X	–	–
78b	USA: UT; Washington Co., Beaver Dam Slope	MOJ/uni.	MVZ 235870	X	X	X	X	–	–
79	USA: UT; Washington Co., Gunlock Reservoir	MOJ/uni.	MVZ 235868	X	X	X	X	X	X
80	USA: UT; Washington Co., Washington	MOJ/uni.	CAS 229948	X	X	X	X	–	–

## Appendix I Continued

Taxon ID	Locality	Region/ Subspecies	Voucher	mtDNA		Nuclear Loci		
				12S	ND4	BDNF	RAG-1	Sun27
<i>Sceloporus orcutti</i>								
1	Mexico: BC; Catavina	SON	ROM 14673	X	X	-	-	
2	Mexico: BCS; San Ignacio	SON	ROM 14377	X	X	-	-	
3	Mexico: BCS; Santa Agueda	SON	ROM 14453	X	X	-	-	
4	Mexico: BCS; San Pedro La Presa	SON	RWM 798	X	X	-	-	
5a	USA: CA; Riverside Co., Diamond Valley	NACR	CAS 201108	X	-	X	X	
5b	USA: CA; Riverside Co., Diamond Valley	NACR	CAS 201124	X	-	X	-	
<i>Sceloporus zosteromus</i>								
1	Mexico: BC; El Rosario	SON/ruf.	MVZ 161290	X	X	X	X	
2a	Mexico: BC; Catavina	SON/ruf.	MVZ 161292	X	X	X	X	
2b	Mexico: BC; Catavina	SON/ruf.	MVZ 161293	X	X	X	X	
3	Mexico: BC; Rosarito	SON/ruf.	MVZ 161311	X	X	X	X	
4	Mexico: BC; Isla Cedros	SON/ruf.	RWM 1890	X	X	-	-	
5	Mexico: BCS; Sierra San Francisco	SON/mon.	MVZ 236294	X	X	X	X	
6	Mexico: BCS; San Antonio	SON/zost.	MVZ 236295	X	X	X	X	
7	Mexico: BCS; Vizcaíno	SON/ruf.	MVZ 236296	X	X	X	X	
8	Mexico: BCS; El Arco	SON/ruf.	JRO 332	X	X	-	-	
9	Mexico: BCS; Isla Monserrate	SON/mon.	RWM 1601	X	X	-	-	
10	Mexico: BCS; La Paz	SON/zost.	MVZ 236297	X	X	X	X	
11	Mexico: BCS; 91 km N of La Paz	SON/mon.	ROM 37006	-	X	-	-	
Outgroup Taxa								
Clarki Group								
	<i>S. clarkii</i>		CAS 229955	X	X	X	X	
Edwardtaylori Group								
	<i>S. edwardtaylori</i>		AM-CC 117980	X	X	X	X	
Formosus Group								
	<i>S. smaragdinus</i>		MVZ 143426	X	X	X	X	
Graciosus Group								
	<i>S. graciosus</i>		BYU 45983	X	X	X	X	
Grammicus Group								
	<i>S. grammicus</i>		UTA R-23970	X	X	X	X	
Maculosus Group								
	<i>S. maculosus</i>		JAM 650	X	X	X	X	
Scalaris Group								
	<i>S. bicanthalis</i>		MZFC 8034	X	X	X	X	
Torquatus Group								
	<i>S. torquatus</i>		UTA R-24016	X	X	X	X	
Variabilis Group								
	<i>S. variabilis</i>		LSUMZ 48723	X	X	X	X	

## Appendix II

Best-fit nucleotide substitution models selected for the mtDNA data partitions and the nuclear loci.

Partition (Model); 12S rRNA + tRNA (GTR + I +  $\Gamma$ ); ND4 first codon positions (GTR +  $\Gamma$ ); ND4 second codon positions (GTR + I); ND4 third codon positions (GTR +  $\Gamma$ ); RAG-1 (HKY + I); BDNF (HKY); *sun27* (HKY + I); *sun32* (HKY).