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Introgression obscures lineage boundaries and phylogeographic history in the western banded gecko, *Coleonyx variegatus* (Squamata: Eublepharidae)

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The geomorphological formation of the Baja California peninsula and the Gulf of California is a principal driver of diversification for the reptiles of North America's warm deserts. The western banded gecko, *Coleonyx variegatus*, is distributed throughout the Mojave, Sonoran and Peninsular deserts. In this study we use multilocus sequence data to address deep phylogeographic structure within *C. variegatus*. Analyses of mtDNA data recover six divergent clades throughout the range of *C. variegatus*. Topology of the mtDNA gene tree suggests separate origins of peninsular populations with an older lineage in the south and a younger one in the north. In contrast, analyses of multilocus nuclear data provide support for four lineages, corresponding to the subspecies *C. v. abbotti*, *C. v. peninsularis*, *C. v. sonoriensis* and *C. v. variegatus*. Phylogenetic analyses of the nuclear data recover *C. v. abbotti* and *C. v. peninsularis* as a clade, indicating a single origin of the peninsular populations. Discordance between the nuclear and mtDNA data is largely the result of repeated episodes of mtDNA introgression that have obscured both lineage boundaries and biogeographic history. Dating analyses of the combined nuclear and mtDNA data suggest that the peninsular clade diverged from the continental group in the Late Miocene.

ADDITIONAL KEYWORDS: Baja California – Mojave Desert – Miocene – reptiles – Sonoran Desert – species tree.

INTRODUCTION

The geological processes behind the formation of the Gulf of California and the isolation of the various landmasses that currently comprise the Baja California peninsula are considered one of the principal causes of diversification of the desert southwest fauna (Riddle & Hafner, 2006). Relative to other vertebrate groups, Baja California squamate reptiles demonstrate particularly high endemism (Orr, 1960; Grismer, 2002). An early biogeographic scenario for the reptiles and amphibians of Baja California hypothesized waves of climate-driven dispersal into an old, stable peninsula (Savage, 1960). Vicariance-based models were later proposed with the subsequent understanding of the geotectonic origin of the peninsula in which the peninsular land elements broke away from the western coast of Mexico and were transferred from the North American plate to the Pacific plate (Seib, 1980; Murphy, 1983). Grismer (1994) proposed a biogeographic model of evolution for the reptiles of the Baja California peninsula that allocated most species into two principle groups. The first group, termed the Southern Miocene Vicariant Complex, contains species that diverged from continental Mexican species when the southern region of the peninsula broke away from the mainland. The second group, the Northern Pliocene Vicariant Complex, comprises species with divergent populations that are parapatric near the head of the Gulf of California. The members of this group are hypothesized to have diverged at the time of the formation of the northern Gulf of California, a geologically more recent event than the southern divergence. This model has provided a basic framework that many subsequent biogeographic studies have used in comparative analyses of other

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vertebrate groups (Riddle *et al.*, 2000). In addition to the formation of the Gulf of California, trans-peninsular marine seaways across both the Isthmus of La Paz and the midpeninsular region may have formed barriers that also shaped diversity on the peninsula (Upton & Murphy, 1997; Aguirre León *et al.*, 1999), and these have also been included in many peninsular phylogeographic models. Despite considerable attention, a coherent biogeographic model that adequately relates the geophysical and climatic evolution of the landscape to temporal and spatial patterns in North American warm desert biota remains elusive, due to uncertainty in the geological data and models, as well as the disparate ways these data are interpreted by biologists (Wilson & Pitts, 2010). This is also the case for events relating to the geological development of the Baja California peninsula (Dolby *et al.*, 2015).

The increased availability of multilocus DNA datasets and newly developed analytical tools facilitates opportunities to better investigate and test competing phylogeographic hypotheses. The feasibility of employing multilocus nuclear sequence data has helped evaluate situations where mitochondrial DNA (mtDNA) sequence data alone gave surprising results. For example, multilocus data provide the opportunity to distinguish among distinct hypotheses regarding patterns of mtDNA gene tree paraphyly, including incomplete lineage sorting (Martínez-Solano *et al.*, 2012), paralogy (Spinks & Shaffer, 2007), imperfect taxonomy (e.g. cryptic species; Leavitt *et al.*, 2007) and interspecific hybridization with subsequent mitochondrial introgression (Good *et al.*, 2008; Bryson *et al.*, 2014). Also, multilocus studies have discovered situations where deep phylogeographic breaks in the mitochondrial genome are not accompanied by similar nuclear differentiation (Ogden & Thorpe, 2002; Pavlova *et al.*, 2013). The need for phylogeographic studies that incorporate multilocus data is well appreciated.

The western banded gecko, *Coleonyx variegatus* (Baird, 1858), is a prominent member of the reptile fauna of the desert south-west, inhabiting the Sonoran, Mojave and Peninsular deserts. In some areas it may be the most frequently encountered nocturnal reptile (Klauber, 1945). Klauber (1945) described seven subspecies: the San Diego banded gecko, *C. v. abbotti*; the desert banded gecko, *C. v. variegatus*; the Tucson banded gecko, *C. v. bogerti*; the Utah banded gecko, *C. v. utahensis*; the Sonoran banded gecko, *C. v. sonoriensis*; the Santa Inés Island banded gecko, *C. v. slevini*; and the San Lucan banded gecko, *C. v. peninsularis*. At the time of description, Klauber hypothesized that broad areas of intergradation characterize regions where different subspecies come into contact. Grismer (2002) similarly concluded that boundaries among subspecies displayed broad clinal variation indicative of extensive gene flow and considered *C. variegatus* a single species, referring to the regional variation described by Klauber as pattern classes rather than subspecies.

While Grismer (2002) considered *C. variegatus* a single species, he previously hypothesized that *C. variegatus* was composed of two distinct lineages (1994). The *abbotti*-group contains the peninsular subspecies *C. v. abbotti*, *C. v. peninsularis* and *C. v. slevini*, while the *variegatus*-group includes the continental subspecies *C. v. variegatus*, *C. v. bogerti*, *C. v. utahensis* and *C. v. sonoriensis*. The subspecies in the *abbotti*-group differ from those in the *variegatus*-group in retaining certain juvenile traits into maturity, namely a smaller size and the juvenile pattern of strong banding with a distinct nuchal loop. Grismer (1994) hypothesized that *C. variegatus* belongs in the younger Northern Vicariant Complex, meaning that peninsular gecko populations diverged from continental populations with the formation of the northern Gulf of California. The peninsular *abbotti*-group and continental *variegatus*-group are hypothesized to have come into secondary contact in north-eastern Baja California where they form a wide intergradation zone south of San Felipe (Grismer, 1994; 2002).

While the probability of Miocene tectonic vicariance influencing phylogeographic structure in *C. variegatus* seems high given the results of recent phylogeographic studies of co-distributed snakes and lizards (Devitt, 2006; Leaché & Mulcahy, 2007, Leavitt *et al.*, 2007), biogeographic scenarios alternative to Grismer's 1994 model are certainly possible. One alternative model could recover an older origin for the southern peninsular subspecies (*C. v. slevini* and *C. v. peninsularis*) that is distinct from a younger origin of the northern peninsular subspecies (*C. v. abbotti*), rejecting the monophyletic peninsular *abbotti*-group. In his initial subspecies descriptions, Klauber (1945) stated that the southern peninsular subspecies are more morphologically similar to the mainland *C. v. sonoriensis* than to *C. v abbotti* or *C. v. variegatus* to the north. A dual origin pattern is observed in the lizard genera *Xantusia* (Sinclair *et al.*, 2004) and *Elgaria* (Leavitt *et al.*, 2017) and the snake genus *Hypsiglena* (Mulcahy & Macey, 2009).

Another biogeographic model is a colonization of the Baja California peninsula from continental populations that postdates the formation of the Gulf of California as terrestrial connectivity at the head of the gulf became more established, which would require a time frame of mid-Pliocene (~4 Mya) or younger (Winker & Kidwell, 1996; Dorsey, 2006). In a study of the ecophysiological evolution of the genus *Coleonyx*, Dial & Grismer (1992) hypothesized that *C. variegatus* diverged from its sister-clade in the

Early Pleistocene, and they presented a biogeographic scenario that requires a geologically young peninsular colonization from continental populations. Welsh (1988) hypothesized such a model for the divergence of the peninsular lizard *Gambelia copeii* (Yarrow, 1882) from the continental *G. wislizenii* (Baird & Girard, 1852), and the results from a phylogenetic analysis of mitochondrial sequence data are consistent with this hypothesis (McGuire *et al.*, 2007). Alternatively, this scenario could be reversed with an 'out-of-Baja' model where a species that had become isolated on the peninsula later expands into neighbouring continental regions via a northern route. Murphy (1983) proposed this model for a number of lizard species, including *Dipsosaurus dorsalis* (Baird & Girard, 1852). Phylogeographic studies of the desert spider *Homalonychus theologus* Chamberlin, 1924 (Crews & Hedin, 2006) and ground squirrel *Ammospermophilus leucurus* (Merriam, 1889) (Mantooth *et al.*, 2013) may also fit this model, with continental regions like the Colorado and Mojave deserts in southern California having been colonized by range expansions derived from the northern peninsular region. Also, a biogeographic model that includes a role for over-water dispersal postdating formation of the Gulf of California should be considered. Phylogeographic studies of snakes have demonstrated that Pleistocene over-water dispersal events are responsible for establishing populations on both the Sonoran and peninsular sides of the gulf (Wood *et al.*, 2008a; de Queiroz & Lawson, 2008); the peninsular iguana *Ctenosaura hemilopha* (Cope, 1863) also appears to have originated via Pleistocene dispersal from coastal Sonora (Davy *et al.*, 2011).

The purpose of this study is to use multilocus DNA sequence data to investigate deep phylogeographic structure within *C. variegatus*. We address whether named subspecies correspond to lineages with separate evolutionary histories and/or if there is unrecognized cryptic diversity. We specifically test the biogeographic model that Grismer proposed for the origin of peninsular Baja California populations relative to those from continental regions.

MATERIAL AND METHODS

TAXON SAMPLING

We collected molecular data from 323 individuals of *C. variegatus* from 120 distinct localities (see Fig. 1), spanning the known range of the taxon. All subspecies are well represented numerically and geographically, except *C. v. slevini*, a taxon from Isla Santa Inés (northeast of Mulegé, BCS) that we were unable to include in this study. Ten individuals of the Texas banded gecko, *C. brevis* Stejneger, 1893, are also included as representatives of the sister-clade to *C. variegatus* (Grismer, 1988). The tissue samples included represent the past efforts of many collectors over the years, as well as fieldwork by the authors specific to this study. Samples and localities are listed in the Appendix.

GENETIC SAMPLING, PHASING OF HAPLOTYPES AND ALIGNMENT

Genomic DNA was extracted from preserved tissue using the DNeasy tissue kit (Qiagen). We included data from two gene regions from the mitochondrial genome. These regions include the NADH subunit 1 (966 base pair bp) and the cytochrome *b* gene (1140 bp). The *ND1* fragment was sequenced for all individuals, and the *Cytb* region was sequenced for a phylogenetically representative subset of 40 individuals. We amplified gene regions from four protein-coding nuclear loci (*BACH1*, *NKTR*, *PRLR* and *R35*), all of which have been used in squamate systematics (Townsend *et al.*, 2008; Wiens *et al.*, 2012). We sequenced *NKTR*, *PRLR* and *R35* for eight *C. brevis* and 200 *C. variegatus*, and *BACH1* for a subset of 50 of those. Primer sequences are available in the Supporting Information (Table S1). Purified PCR products were sequenced using the same primers as the PCR reactions except for *BACH1*, where we used internal primers. The electropherogram data were verified and edited with SEQUENCHER 4.7 (Gene Codes Corp., Ann Arbor MI). All gene regions in this study are protein coding, and alignment was straightforward and performed in SEQUENCHER. We resolved haplotypes for nuclear gene sequences using the programs SeqPHASE (Flot, 2010) and PHASE v.2.1.1 (Stephens *et al.*, 2001; Stephens & Donnelly, 2003), using the most probable haplotypes for subsequent analyses.

MITOCHONDRIAL AND NUCLEAR GENE TREES

To infer the mtDNA gene tree, the *ND1* matrix with redundant haplotypes removed was concatenated with the *Cytb* data. We partitioned the data by codon position (first, second, third) and used jModelTest (Posada, 2008) to identify models of sequence evolution using the AIC. Subsequent phylogenetic analyses were performed on both the total concatenated dataset and a smaller mtDNA dataset using only individuals represented by both fragments. Maximum likelihood (ML) analyses were performed with RAxML v.7.2.8 (Stamatakis *et al.*, 2008) via the CIPRES Science Gateway (Miller *et al.*, 2011), using the GTR+Γ model for each partition and automatic bootstrapping. Bayesian analyses were performed with the program BEAST v.1.8 (Drummond & Rambaut, 2007) and were also partitioned by codon position. The BEAST mtDNA analyses employed an uncorrelated

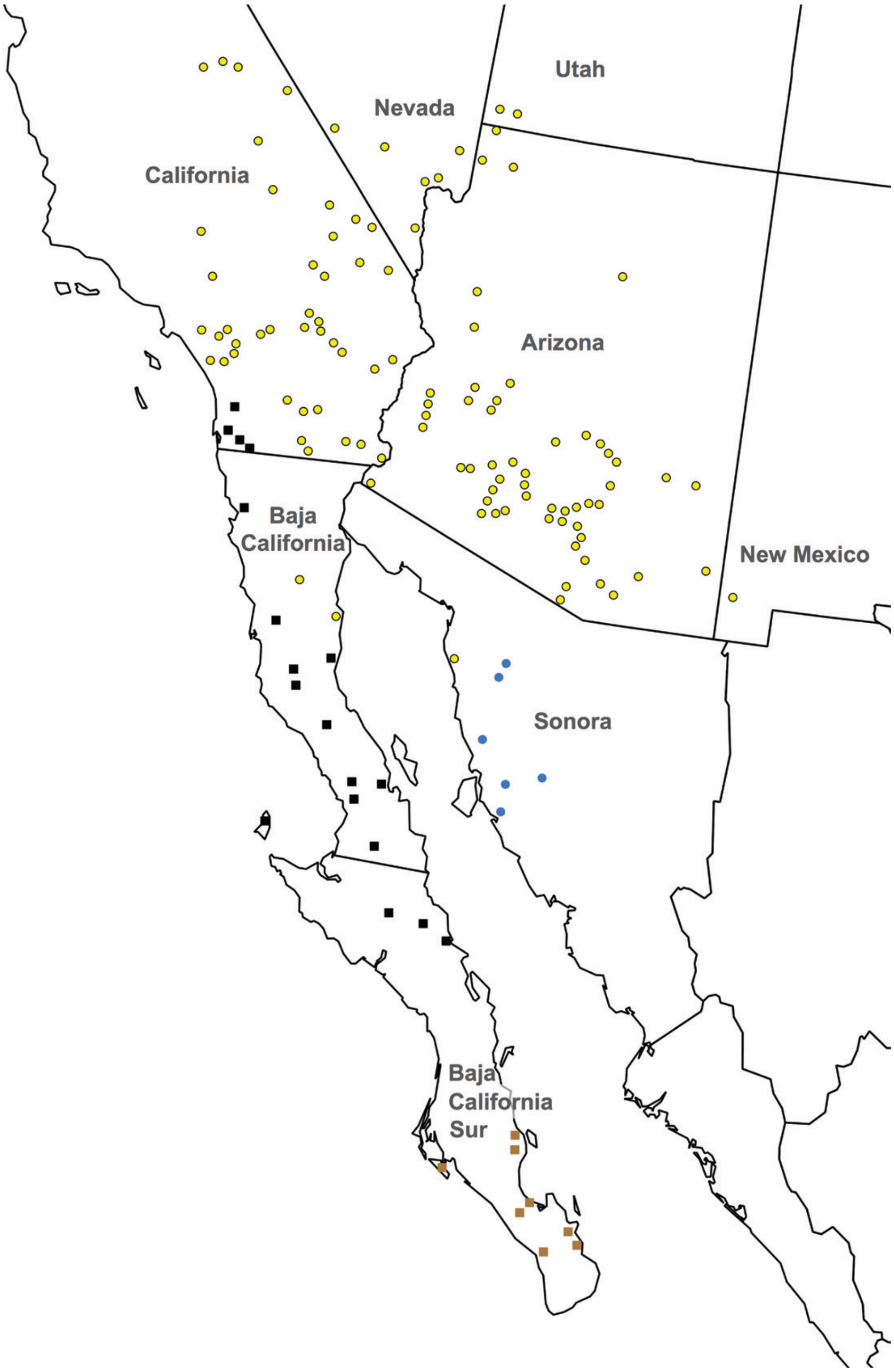

Figure 1. Locations of sampled *Coleonyx variegatus*. Locality symbols represent membership inferred from nuclear data. Squares represent the *abbotti*-group and circles the *variegatus*-group. Colours correspond to genetically inferred lineages: *Coleonyx variegatus variegatus* in yellow, *C. v. sonoriensis* in blue, *C. v. abbotti* in black, and *C. v. peninsularis* in brown.

lognormal relaxed clock and a coalescent tree prior. BEAST analyses were run multiple times, with 150 million generations per analysis saving every 3000th generation. TRACER v.1.5 (Rambaut & Drummond, 2007) was used to assess convergence and remove the appropriate number of generations as burn-in. We inferred topologies of the nuclear loci via maximum-likelihood analyses of nuclear genes that were also performed with RAxML on CIPRES using the GTR+Γ model for each gene without partitioning.

MULTILOCUS CLUSTERING ANALYSES

To identify lineage composition, we employed the program POFAD (Phylogeny of Organisms From Allelic Data; Joly & Bruneau, 2006) to identify clusters using the multilocus nDNA dataset. POFAD accommodates allelic variation (as well as missing data) to create a single genetic distance matrix from the separate matrices from multiple gene regions; all loci are weighted equally to calculate a standardized matrix. Uncorrected p-distance matrices for the four individual nuclear loci were calculated using PAUP* (Swofford, 2002). We analysed the combined, standardized nDNA distance matrix using both network and distance-based phylogenetic approaches. We created an unrooted network with the Neighbor-net method using SplitsTree v.4.13.1 (Hudson & Bryant, 2006). Distance-based tree topologies were also inferred using both Neighbor-joining (NJ) and Unweighted Pair Group Method with Arithmetic Mean (UPGMA) in PAUP*. To evaluate the robustness of the clustering inferred by this approach, we used a nonparametric bootstrapping procedure similar to that of Spinks *et al.* (2010). For each locus, the Seqboot module within PHYLIP 3.66 (Felsenstein, 2005) was used to create 100 nonparametric pseudoreplicate datasets for each of the four nuclear loci. From each pseudoreplicate dataset, a single standardized matrix was calculated with POFAD, which was then used to create a UPGMA tree in PAUP*. A majority-rule consensus tree was then generated using the 100 bootstrap topologies.

SPECIES TREE ANALYSES

Species tree inference was performed with *BEAST (Heled & Drummond, 2010) as implemented in BEAST v.1.8, using the clusters identified with the nuclear POFAD analyses. We used the substitution model HKY+Γ and an uncorrelated lognormal relaxed clock for each nuclear locus and the default Yule tree prior. *BEAST analyses were run for 300 million generations with every 5000th saved. Analyses were run multiple times to confirm convergence of independent analyses. TRACER was used to assess stationarity and confirm that ESS scores for estimated parameters were >200 (Rambaut & Drummond, 2007). Species tree inference was performed with both a nuclear-only dataset, as well as a combined nDNA and mtDNA dataset. Given that hybridization can both mislead and distort species trees (Heled *et al.*, 2013; Leaché *et al.*, 2014; Leavitt *et al.*, 2017), analyses were performed with original configurations, as well as with hypothesized introgressed genes reassigned (see below).

One of the approaches that we used to evaluate hypotheses of incomplete lineage sorting versus introgression is the Bayes factor delimitation (BFD) method of Grummer *et al.* (2014) that was modified by Leavitt *et al.* (2017). Rather than reassigning individuals among species as was done with the original BFD method, in the modified approach only the specific alleles hypothesized to have introgressed are reassigned. The estimated marginal likelihoods from the *BEAST analyses of the two arrangements were compared with the stepping-stone and path sampling methods (1 000 000 generations and 100 path steps; Xie *et al.*, 2011, Baele *et al.*, 2012). The recommendations of Kass & Raftery (1995) were used to calculate Bayes factors to determine which of two competing models is favoured. We first used this method with the complete nuclear-only dataset. In this analysis, for the individual nuclear gene trees we identified alleles hypothesized to have introgressed based on two criteria. First, alleles were considered introgressed when they were recovered as 'misplaced' at tip positions in clades comprised of individuals of a neighbouring lineage. Second, alleles were required to be geographically proximate to regions of hypothesized secondary contact. The use of these criteria was a conservative approach, and not all instances of non-monophyly were treated as introgression. We performed analyses with two arrangements: the first assumed no introgression and thus no alleles were reassigned, while the second arrangement reassigned the hypothesized introgressed alleles to the donor species.

Discordance between the mitochondrial gene tree and the multilocus analyses of nDNA recovered instances of gene tree/species tree conflict where it was not obvious whether ancient mitochondrial capture or incomplete lineage sorting (ILS) was responsible (see Results). To test hypotheses of ancient mitochondrial capture vs. ILS, we performed analyses similar to those above, where we either assumed ILS-only and no alleles were reassigned or where mtDNA alleles thought to have experienced mitochondrial capture were reassigned to the donor species (see Results). The dataset used in these analyses consisted of 50 individuals that had complete data for all four nuclear loci and 40 individuals with both mtDNA fragments. The concatenated mtDNA data were partitioned by codon position and a relaxed lognormal molecular clock. These species tree analyses and the accompanying stepping-stone and path sampling were run as above.

Additional tests of introgression

We also used a second method to evaluate whether ancient mitochondrial capture or incomplete lineage sorting was the best explanation of discordance between the mtDNA gene tree and the nuclear species tree (Leavitt *et al.*, 2017). In this approach, we assessed the relative fit of the mtDNA topology to the nuclear-derived species tree for the various competing hypotheses by calculating the cost of the different hypotheses by summing the total number of discordant events needed to reconcile the mtDNA gene tree to the species tree (Page & Charleston, 1997). For the incomplete lineage sorting hypothesis, all discordance is due to ILS and the number of extra gene lineages for each single branch was summed for the total of all branches of the species tree (Maddison, 1997). For hypotheses of 'mitochondrial capture', the branch subtending haplotypes hypothesized to have introgressed was pruned and transferred to the receiving lineage prior to minimizing deep coalescent events when fitting the mtDNA gene tree to the nDNA species tree. Each pruning and transfer represented an instance of introgression. The number of deep coalescences was then summed with the number of introgressive events to arrive at the total cost of the respective scenario. A parsimony optimality criterion was used to determine which scenario was the best fit, favouring the fewest total discordant events. For this approach, we calculated discordant events in two different ways. The first analysis considered only the topologies when fitting the mtDNA gene tree to the nuclear species tree. In addition to topological constraints, the second analysis also maintained proportional branch lengths of the mtDNA gene tree relative to those of the nDNA based species tree (as inferred in their respective BEAST and *BEAST analyses) when calculating the fit of the embedded gene tree. We will refer to these approaches as gene-fitting topology only and gene-fitting with proportional branch lengths.

Divergence dating

Divergence dating using the combined nDNA and mtDNA data was also performed in *BEAST. This analysis used the preferred configuration of the combined data as identified by the introgression analyses. The genus *Coleonyx* and the family Eublepharidae lack a fossil record that could contribute calibration points for estimating divergence times with molecular data. Despite considerable attention, well-supported substitution rates for squamate reptiles remain somewhat elusive. We used a mitochondrial substitution rate of 1.55% Myr^{-1} estimated in a clade of gekkotan lizards (Siler *et al.*, 2012). Dating analyses were performed with the reduced dataset of 50 individuals with complete nuclear data and the 40 with complete mtDNA data. Species tree analyses were performed with the same conditions as those described in section SPECIES TREE ANALYSES above, with mitochondrial clades hypothesized to have experienced introgression assigned to the donor species.

RESULTS

Properties of molecular data

The DNA sequence data generated for this study have been submitted to GenBank (see Appendix). For the six sequenced gene fragments, Table 1 reports the number of individuals sequenced for each gene (including outgroups), the aligned length of each locus, the number of unique haplotypes and other relevant information, including the proportion of heterozygous individuals for the nuclear loci.

Mitochondrial gene tree

Initial partitioned BEAST analyses of the concatenated mitochondrial *ND1* and *Cytb* genes using the preferred GTR models selected by jModelTest failed to reach stationarity as certain parameters were difficult to estimate. Subsequent BEAST analyses of the

Table 1. Information for the six gene fragments including number of individuals sequenced and relative information content

	Number Sequenced	Unique Haplotypes	Aligned length	Parsim. Informative	Parsimony Uninformative	Percent Heterozygous
NADH subunit 1	334	255	966	272	51	NA
Cytb	38	38	1140	379	66	NA
BACH1	55	56	922	47	33	67%
NKTR	208	122	525	59	24	69%
PRLR	208	185	544	80	31	68%
R35	208	194	570	76	29	84%

partitioned mtDNA data used the HKY+Γ for each of the three codon positions. The partitioned maximum-likelihood analyses performed in RAxML did use GTR+Γ models and recovered an identical topology to the Bayesian BEAST analyses with respect to the major clades. The Bayesian and ML analyses of mtDNA sequence data recover six divergent, allopatric haploclades throughout the sampled range of *C. variegatus*, with neither the peninsular *abbotti*- nor the continental *variegatus*-groups being recovered as monophyletic (Figs 2, 3). Relationships among major clades and subclades are well supported [Posterior Probability (PP)≥0.95], except for one relatively basal node (PP = 0.78): clade VI occurring in the southern Baja California peninsula was recovered as sister to the other five, but without strong support in both Bayesian and ML analyses. Clades V and IV received strong support as sister lineages. Both are distributed in the northern Mojave Desert; clade V contains closely related haplotypes from Inyo County, California, and the distribution of clade IV includes south-western Utah, north-western Arizona, southern Nevada and eastern San Bernardino County, California. Clade III has a central peninsular distribution, with sampled localities from near Cataviña south through the Vizcaíno Desert to just south of Santa Rosalía. Clade II includes most samples from Sonora, Mexico. Clade I is geographically widespread, being found throughout most of the Mojave Desert in California (clade IA), the Sonoran Desert in Arizona (clades IB1, IB2, IB3) and north-western Sonora (clade IB4), the Colorado Desert in southern California and north-eastern Baja California, as well as coastal southern California and north-western Baja California (clade IB5). Populations hypothesized to belong to the peninsular *abbotti*-group include those in clade VI (subspecies *C. v. peninsularis*), clade III (subspecies *C. v. abbotti* and hypothesized intergrades with *C. v. peninsularis*) and subclades IB5ai, IB5aii and IB5bi of the widespread clade (subspecies *C. v. abbotti*).

NUCLEAR DATA

The Neighbor-net based network inferred from the standardized POFAD nDNA distance matrix is illustrated in Figure 4A. The principle clusters inferred from the network were corroborated with the additional distance analyses in PAUP* (Fig. 4B). In contrast to the mtDNA data, analyses of the nDNA recover well-supported distinct clusters corresponding both to the continental *variegatus*-group and to the peninsular *abbotti*-group, with one modification. Rather than clustering with other members of the peninsular subspecies *C. v. abbotti*, geckos sampled from coastal California in north-western San Diego, Orange and Riverside counties cluster with the continental *variegatus*-group. These same individuals belong to the mitochondrial clade IB5bi. Within the peninsular cluster, there are two subgroups. A southern cluster is composed of individuals from mitochondrial clade VI and falls within the distribution of the subspecies *C. v. peninsularis*. A northern cluster consisting of individuals belonging to the mtDNA clades III, IB5ai and IB5aii is generally equivalent with the subspecies *C. v. abbotti* with the principle exception noted above. Additionally, individuals sampled from the midpeninsular region (a hypothesized *peninsularis*–*abbotti* intergrade zone) group with this northern peninsular cluster as they did with the mtDNA data. Within the continental *variegatus*-group, the Neighbor-net, NJ and UPGMA analyses recover a well-supported group consisting of all but one of the individuals from Sonora, Mexico. This cluster corresponds closely to the subspecies *C. v. sonoriensis* and includes individuals from mtDNA clade II and all but one individual of clade IB4. The remaining members of the continental group form an identifiable cluster in both the Neighbor-net network and the NJ topology, which recovers these individuals in a clade sister to the Sonoran one. This group includes individuals from the mtDNA clades V, IV and most of I (with the exceptions noted above). Following analyses of the combined nuclear distance matrix, the four clusters from Figure 4 are treated as distinct OTUs in subsequent species tree analyses. These taxa will hereafter be referred to as *C. v. abbotti*, *C. v. peninsularis*, *C. v. sonoriensis* and *C. v. variegatus*. These four groups are geographically cohesive and exclusive with the current sampling.

Individual nuclear gene trees naturally display less resolution than the mtDNA tree, but phylogenetic information is clearly apparent in some relationships (Supporting Information, Fig. S1A–D). In three of the four genes (*BACH1*, *NKTR* and *R35*), the individuals from the peninsular *abbotti*-group formed a clade (with a couple of exceptions mentioned below). In the *PRLR* gene tree, *C. v. abbotti* and *C. v. peninsularis* were each largely recovered as distinct clades, although neither species-group was recovered as monophyletic. Individuals of *C. v. sonoriensis* generally clustered together, although the only gene that recovered them as a single clade was *NKTR*. In two of the genes (*PRLR* and *R35*), there was evidence of some non-exclusivity where the peninsular and continental groups are in proximity in both north-eastern Baja California and coastal California. This pattern also existed for three of the genes in relation to the *C. v. sonoriensis* and *C. v. variegatus* clusters in Sonora. In these instances, 'misplaced' alleles generally have a 'tip' position in the gene tree and are also proximate to sampled individuals of the 'correct' cluster. The number of misplaced alleles for each gene is as follows: two for *BACH1*, both near the Sonoran contact zone in the vicinity of Caborca; no instances for *NKTR*; eight for *PRLR*, two of which

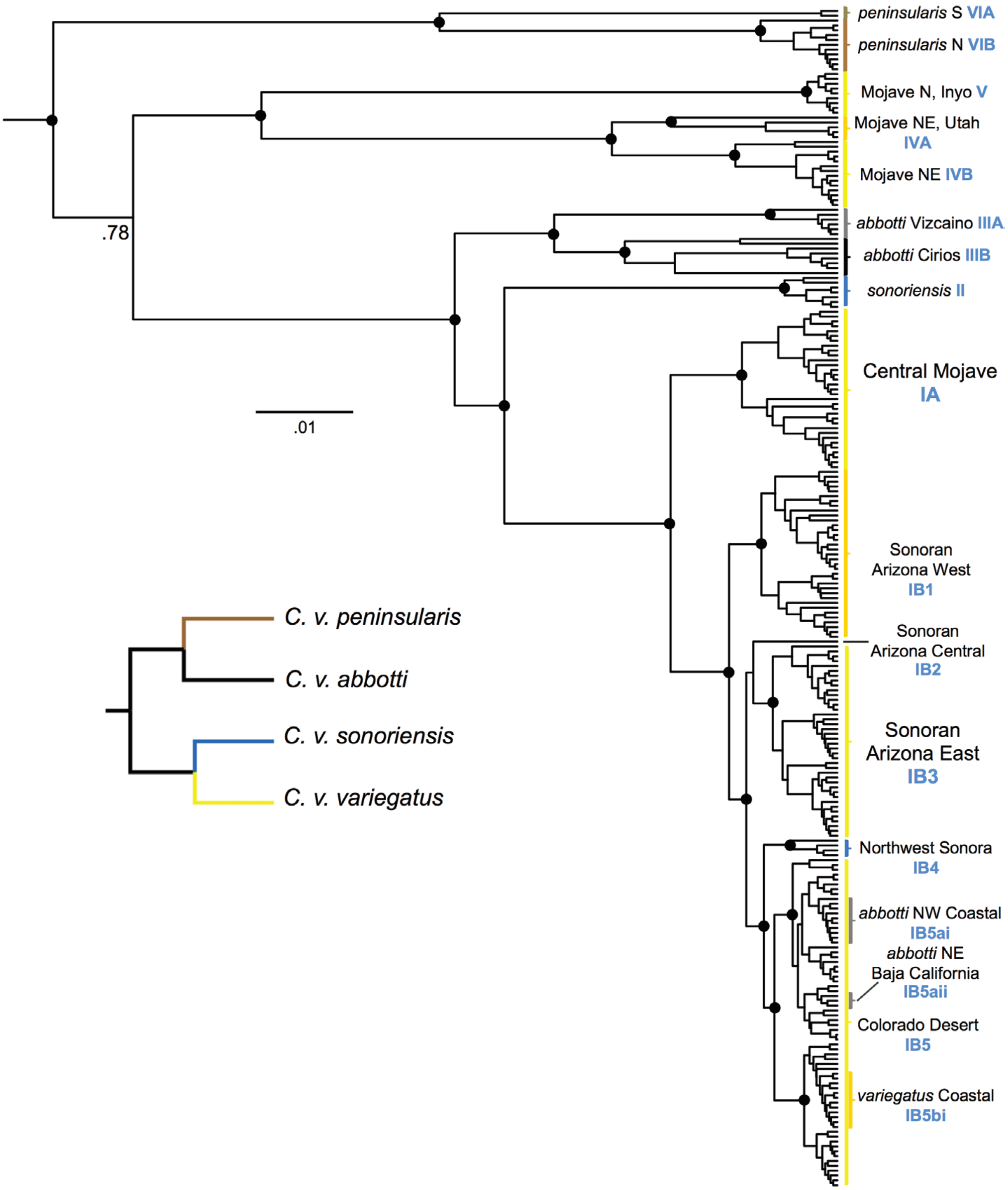

Figure 2. Maximum clade credibility tree from the mtDNA BEAST analysis inferred from concatenated *ND1* and cytochrome *b* fragments. Bayesian posterior probabilities at major nodes are indicated with black dots for well-supported nodes (PP ≥ 0.95) and others with corresponding value listed. Branch to the outgroup *C. brevis* not shown. *Coleonyx v. variegatus* clades are in yellow, *C. v. sonoriensis* in blue, *C. v. abbotti* in black and grey, *C. v. peninsularis* in brown. Certain relevant subclades are labelled, including those resulting from introgression. Inset image depicts relationships inferred by nuclear species tree analyses for reference (see results).

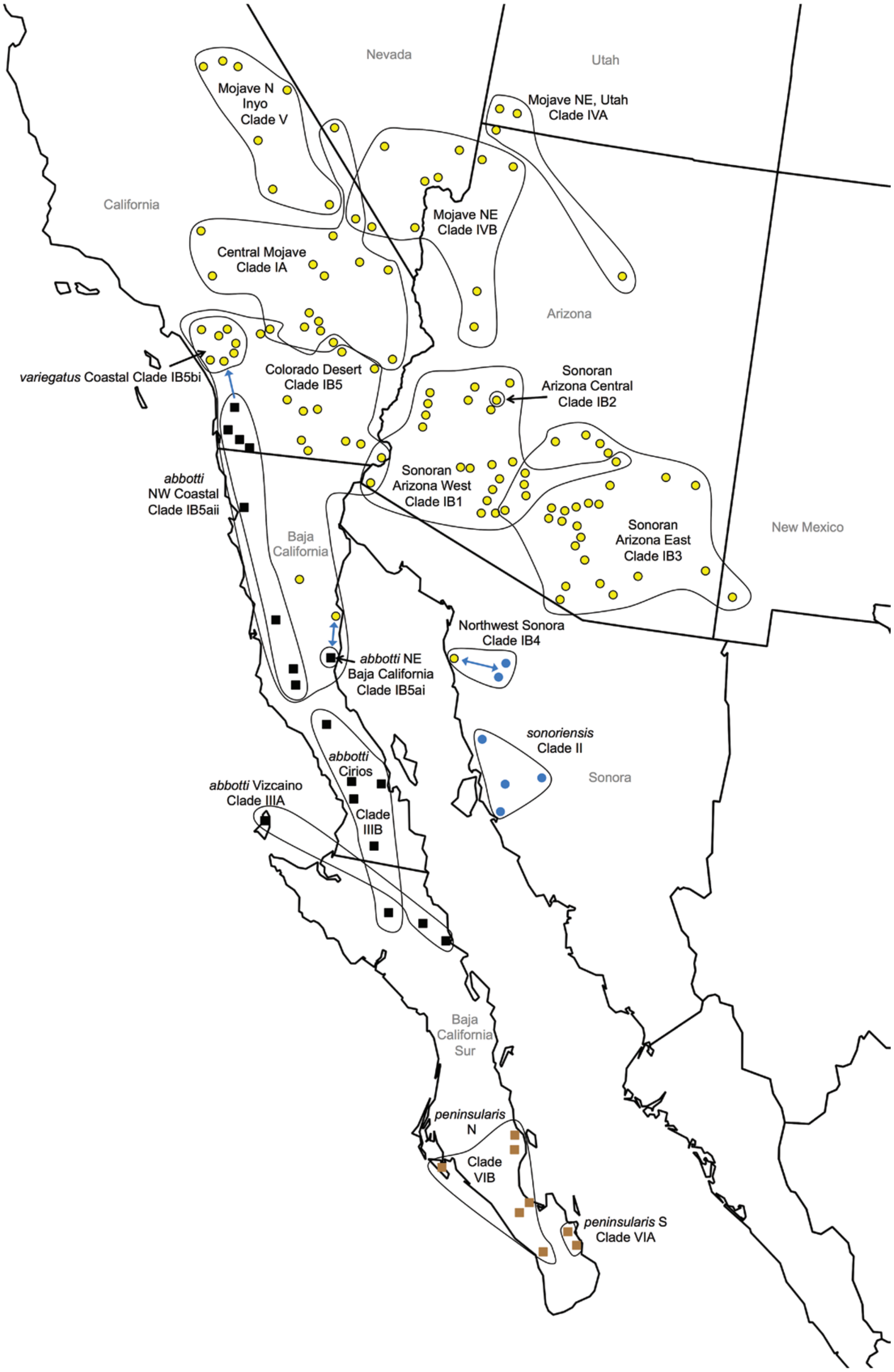

Figure 3. Geographic distribution of mitochondrial lineages (circled) and nuclear lineages (by colour). *Coleonyx variegatus variegatus* in yellow, *C. v. sonoriensis* in blue, *C. v. abbotti* in black, *C. v. peninsularis* in brown. Labels refer to haploclades depicted in Figure 2. The blue arrows indicate the direction of detected nuclear introgression.

are in southern California, four in north-eastern Baja California and two in Sonora; and two for *R35*, one in north-eastern Baja California and one in Sonora.

*BEAST species tree analyses with the full nuclear-only dataset recovered the same topology under both the 'no reassignment' and the 'misplaced' alleles reassigned configurations (Fig. 5), and this inferred species tree is also consistent with the shape of the topologies inferred in the distance analyses of the combined nuclear data (Fig. 4). However, the estimated posterior probabilities and branch lengths differed for the two arrangements. In the arrangement where alleles are left in their original cluster (Fig. 5A), neither the continental group nor the peninsular group are well supported (posterior probabilities of 0.52 and 0.69, respectively), whereas these relationships are recovered with strong support (PP ≥ 0.99) in the species trees based on the reassignment of the twelve introgressed alleles (Fig. 5B). The branch length ratio of crown *C. variegatus* relative to the root is 26% shorter in the unmodified arrangement versus the one where alleles are reassigned. The results of the modified BFD test with the nuclear data favours introgression as the source for discordance. The estimated Bayes factors indicate decisive support (e.g. 2lnBf > 10) for the model where introgression is assumed and haplotypes are reassigned relative to the no introgression hypothesis (see Table 2).

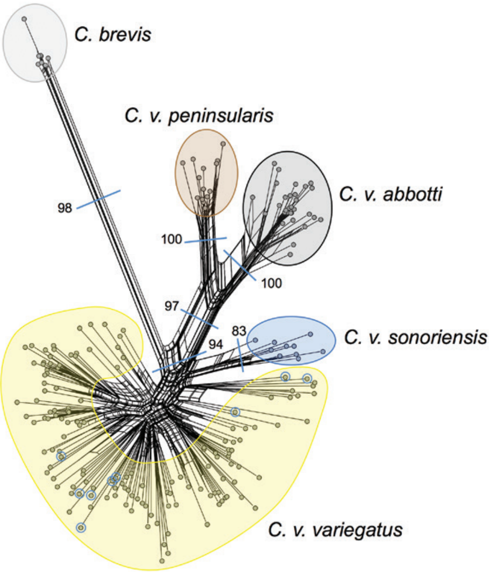

Figure 4. (A) Network of the combined nuclear data as analysed by POFAD and Neighbor-net analyses. Clusters also recovered by the UPGMA bootstrap analysis are indicated by blue bars accompanied with bootstrap values. *Coleonyx v. variegatus* individuals from mtDNA cluster IB5bi that were previously hypothesized to belong to the taxon *C. v. abbotti* are circled. (B) Neighbor-joining analysis of the POFAD-analysed combined nuclear dataset. The four recovered lineages are indicated by the bars on the right: *Coleonyx variegatus variegatus* with the yellow bar, *C. v. sonoriensis* the blue, *C. v. abbotti* the black, and *C. v. peninsularis* the brown. Individual labels correspond to traditionally understood subspecific arrangement. Of particular note are individuals from the subspecies *C. v. bogerti* (orange) and *C. v. utahensis* (gold), here considered conspecific with *C. v. variegatus*.

Figure 4. Continued

ANCIENT MITOCHONDRIAL CAPTURE OR INCOMPLETE LINEAGE SORTING

The mitochondrial clades IB4, IB5ai and IB5aii are sources of gene tree/species tree discordance that we infer to be the result of mitochondrial introgression, given their highly nested and shallow positions within the widespread *C. v. variegatus* mtDNA clade I and their geographic proximity to lineage boundaries recovered by the nuclear data. Explicit empirical tests were not performed for these obvious instances of introgression. We evaluated three different hypotheses with both the modified BFD analyses and the gene-fitting methods. The first hypothesis assumed incomplete lineage sorting (ILS only) as the sole source of discordance between the inferred mtDNA gene tree and the nuclear-inferred species tree and no mtDNA was reassigned. The second hypothesis assumed that the difference between the relative position of the *C. v. abbotti* mtDNA clade III and the nuclear-only species tree was due to a single instance of ancient mitochondrial capture; this species tree analysis assigned mtDNA clade III to *C. v. variegatus* as the hypothesized donor. The third hypothesis assumed two instances of ancient mtDNA capture: one involving the *C. v. abbotti* mtDNA clade III and the second involving the *C. v. variegatus* mtDNA clade I; this species tree analysis assumed *C. v. sonoriensis* as the donor of both mtDNA clades I and III. The results of the modified BFD test favoured the third hypothesis, with the estimated Bayes factors indicating decisive support (e.g. 2lnBf > 10) for the species tree arrangement with two instances of ancient mtDNA capture (see Table 3).

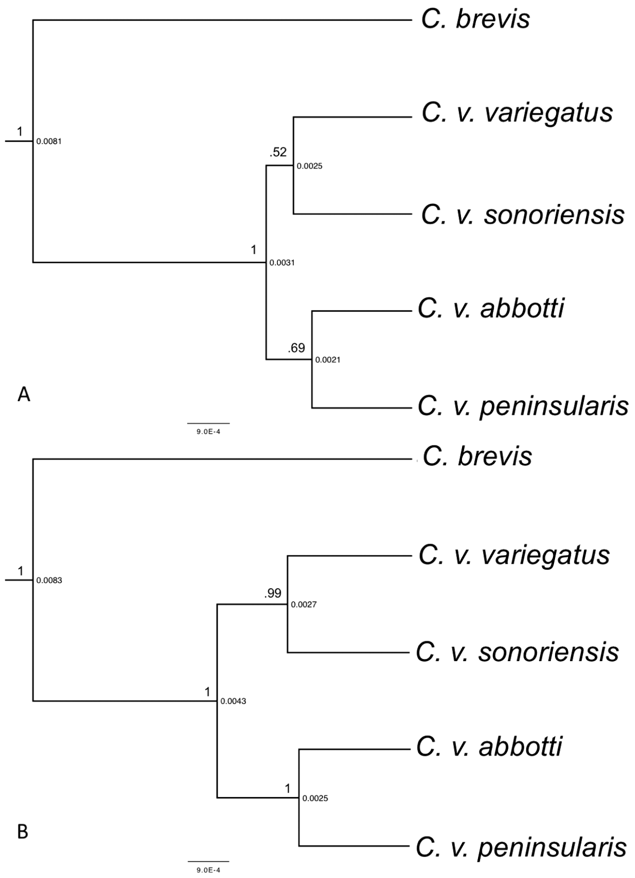

Figure 5. Maximum clade credibility trees from *BEAST without reassigning alleles (A) and with hypothesized introgressed alleles reassigned (B), with posterior probabilities. Branch lengths estimated relative to the locus *BACHI* with an assigned rate of one substitution per site.

We also tested the same three hypotheses with the gene-fitting approach (Table 3). Using the gene-fitting topology-only method, the first hypothesis, ILS only, required three discordant events. This method did not discriminate between the second and third hypotheses, with both having a cost of two discordant events. Using the gene-fitting with proportional branch lengths resulted in a cost of eight discordant events for the ILS only hypothesis, whereas the second hypothesis (a single ancient mtDNA capture) had a better score with five (four instances of ILS + one introgression). The third hypothesis (two assumed instances of ancient mtDNA capture) had the best score, with only three discordant events required (one instance of ILS + two introgression). Additionally, the scenario where all discordance is due to incomplete lineage sorting pushes the mitochondrial crown of *C. v. variegatus* past the nuclear species tree divergence with *C. brevis*. In this arrangement, the relative age of the *variegatus–brevis* mitochondrial divergence would

Table 2. Marginal likelihood scores and Bayes factors for *BEAST analyses that evaluate parapatric nuclear introgression in *C. variegatus* lineages

	Path Sampling		Stepping Stone	
	ln(Marginal Likelihood)	2ln[BF]	ln(Marginal Likelihood)	2ln[BF]
No Introgression	-13 965.0	280.8	-14 016.3	251.8
Introgression	-13 824.6	-	-13 890.4	-

be more than twice as old as the nDNA-only inferred species tree divergence. This suggests that the amount of gene tree/species tree discordance in the ILS only scenario is underestimated in this approach as greater gene tree-species tree discordance would be detected if other *Coleonyx* species had been included as outgroups.

DIVERGENCE DATING

Because tests of introgression favoured ancient mtDNA capture as the source of incongruence, the combined mtDNA and nDNA dataset used in dating analyses had introgressed mtDNA lineages reassigned. As with the preferred species tree analysis of the nuclear-only dataset, the species tree analyses of the combined

Table 3. Evaluation of ancient mitochondrial capture versus ILS in *C. variegatus.* Results of gene-fitting (both topology-only and using relative branch lengths). Marginal likelihood scores from Path Sampling and Stepping Stone analyses in *BEAST and associated Bayes factors are also given

		Discordant Events				
Model	Topology	Branch Lengths	PS MLE	BF	SS MLE	BF
A. ILS only	3 (3 ILS)	8 (8 ILS)	−19 800.03	+16.7	−19 805.69	+17.4
B. 1 Ancient mt capture	2 (1 MC + 1 ILS)	5 (1 MC + 4 ILS)	−19 814.77	+46.2	−19 808.59	+23.2
C. 2 Ancient mt capture	2 (2 MC)	3 (2 MC + 1 ILS)	−19 791.68	–	−19 796.99	–

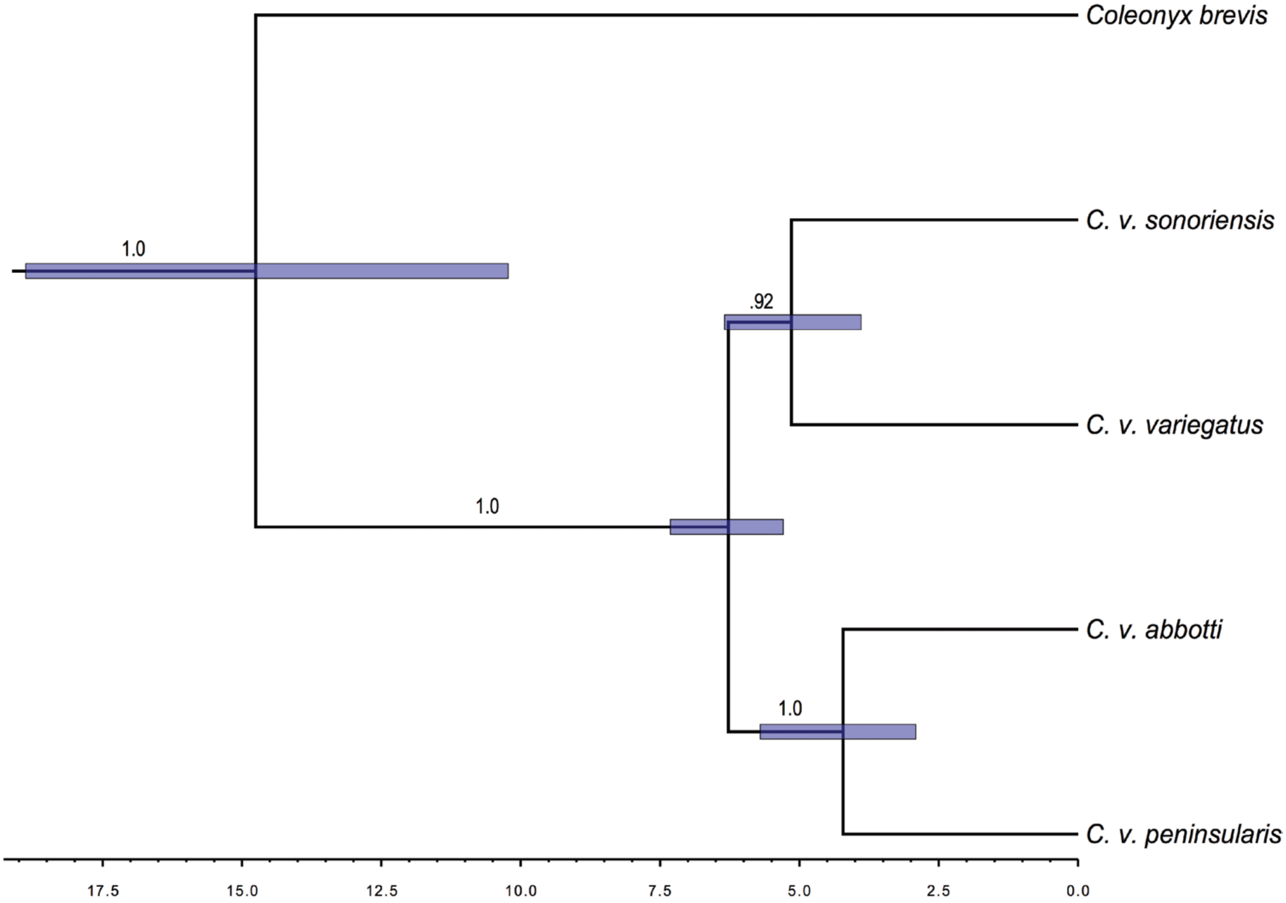

Figure 6. Maximum clade credibility tree of combined mtDNA and nDNA *BEAST species tree analysis. Posterior probabilities are indicated at each node, and 95% confidence interval of age estimates are indicated with blue bars. Scale is in millions of years.

nDNA and mtDNA data also recover both a peninsular *abbotti*-group and a continental *variegatus*-group (Fig. 6), although the continental group received only marginal support (PP = 0.92). The estimated divergence of these groups is 6.28 Mya (5.29–7.32 Mya). Other divergence estimates include 14.75 Mya (10.22–18.88 Mya) for the divergence of *C. brevis* and *C. variegatus*, 5.14 Mya (3.89–6.34 Mya) for the divergence of *C. v. variegatus* and *C. v. sonoriensis* and 4.22 (2.76–5.5 Mya) for the divergence of *C. v. abbotti* and *C. v. peninsularis*. The mitochondrial gene tree inferred from this analysis also provides estimates of when ancient mitochondrial introgressive events may have occurred: sometime between 2.38 and 3.16 Mya for the *C. v. abbotti* clade III and 1.27 and 2.71 for the *C. v. variegatus* clade I. The introgressive events that led to mtDNA clades IB4, IB5ai and IB5aii are young, dating to the Late Quaternary.

DISCUSSION

LINEAGE BOUNDARIES

Both the clustering and species tree analyses of the nuclear data provide support for Grismer's hypothesis of distinct peninsular *abbotti*- and continental *variegatus*-groups. Analyses of this multilocus dataset also infer that four lineages within *C. variegatus* merit taxonomic recognition: *C. v. variegatus*, *C. v. sonoriensis*, *C. v. abbotti* and *C. v. peninsularis*. While three of the four lineages correspond near perfectly to named subspecies, genetic data reveal the previously taxonomic understanding as imperfect. Notably, the coastal California populations from the area including western Riverside County belong to the continental *C. v. variegatus* lineage rather than the peninsular *C. v. abbotti* (Fig. 7). While these four taxa represent unique, deeply divergent lineages that may merit species recognition, we retain these taxa as subspecies until genetic interaction at contact zones is more thoroughly characterized (Hillis, 2019). Also, the analyses of these data indicate that populations belonging to continental subspecies *C. v. utahensis* and *C. v. bogerti* are not deeply differentiated from *C. v. variegatus* (Fig. 4B). We thus consider *C. v. utahensis* and *C. v. bogerti* to be conspecific with *C. v. variegatus,* but we refrain from explicitly synonymizing these taxa with *C. v. variegatus* pending additional study.

Molecular phylogeographic studies of widespread geckos have revealed considerable unrecognized diversity; many nominal species appear to be complexes of multiple species, many of which are cryptic and some surprisingly old (e.g. Pepper *et al.*, 2006; Doughty *et al.*, 2010; Fujita *et al.*, 2010; Geurgas & Rodrigues, 2010; Oliver *et al.*, 2010; Werneck *et al.*, 2012). Within *Phyllodactylus*, the other Baja California gekkotan representative, a phylogeographic analysis confirmed a single origin for the three peninsular species (Blair *et al.*, 2009), although these geckos likely belong to the group of reptiles with an older southern vicariant origin (Grismer, 1994). While the four recovered lineages within *C. variegatus* are not morphologically cryptic given their previous recognition as named subspecies, the treatment of *C. variegatus* as a single taxon clearly misrepresents true lineage diversity. Also, the results of this study reveal that *C. v. abbotti* has a much more limited distribution in California (Fig. 7), and this refined understanding was considered in re-evaluating the conservation status of this taxon within the state, leading to the listing of *C. v. abbotti* as a California Species of Special Concern (Thomson *et al.*, 2016).

It was previously hypothesized that areas where *C. v. abbotti* comes into contact with both *C. v. peninsularis* and *C. v. variegatus* form broad intergrade zones (Klauber, 1945; Grismer *et al.*, 1994; Grismer, 2002). These data provide evidence for limited bidirectional nuclear gene flow between *C. v. abbotti* and *C. v. variegatus* (Fig. 7), as well as unidirectional mtDNA introgression into *C. v. abbotti*. Instead of a broad intergrade zone, a more thorough investigation of one of these areas of secondary contact finds a narrow hybrid zone with strong barriers to gene flow (Leavitt *et al.*, in prep.). While hybridization among gecko species has not been extensively documented, a hybrid zone between two Puerto Rican *Sphaerodactylus* species is similarly narrow (Pinto *et al.*, 2019). This study also demonstrates limited gene flow in the area of contact between *C. v. variegatus* and *C. v. sonoriensis*, and further work should better characterize hybridization between these two taxa with increased geographic and genetic sampling.

Multiple questions remain to be addressed with additional taxonomic and geographic sampling within this group. For one, a test of the genetic distinctiveness of the insular subspecies *C. v. slevini* from Isla Santa Inés relative to the peninsular populations has yet to be performed. Also, this study lacks samples of *C. v. peninsularis* from their northern distribution, including the area near Mulegé and Loreto. Additional work will target this area to identify the boundary between *C. v. peninsularis* and *C. v. abbotti* (Grismer *et al.*, 1994) and to characterize the degree of reproductive isolation.

PHYLOGENETIC RELATIONSHIPS AND MITO-NUCLEAR DISCORDANCE

Once the introgression at secondary contact is accounted for, species tree analyses of the four nuclear loci recover a well-supported topology that recovers

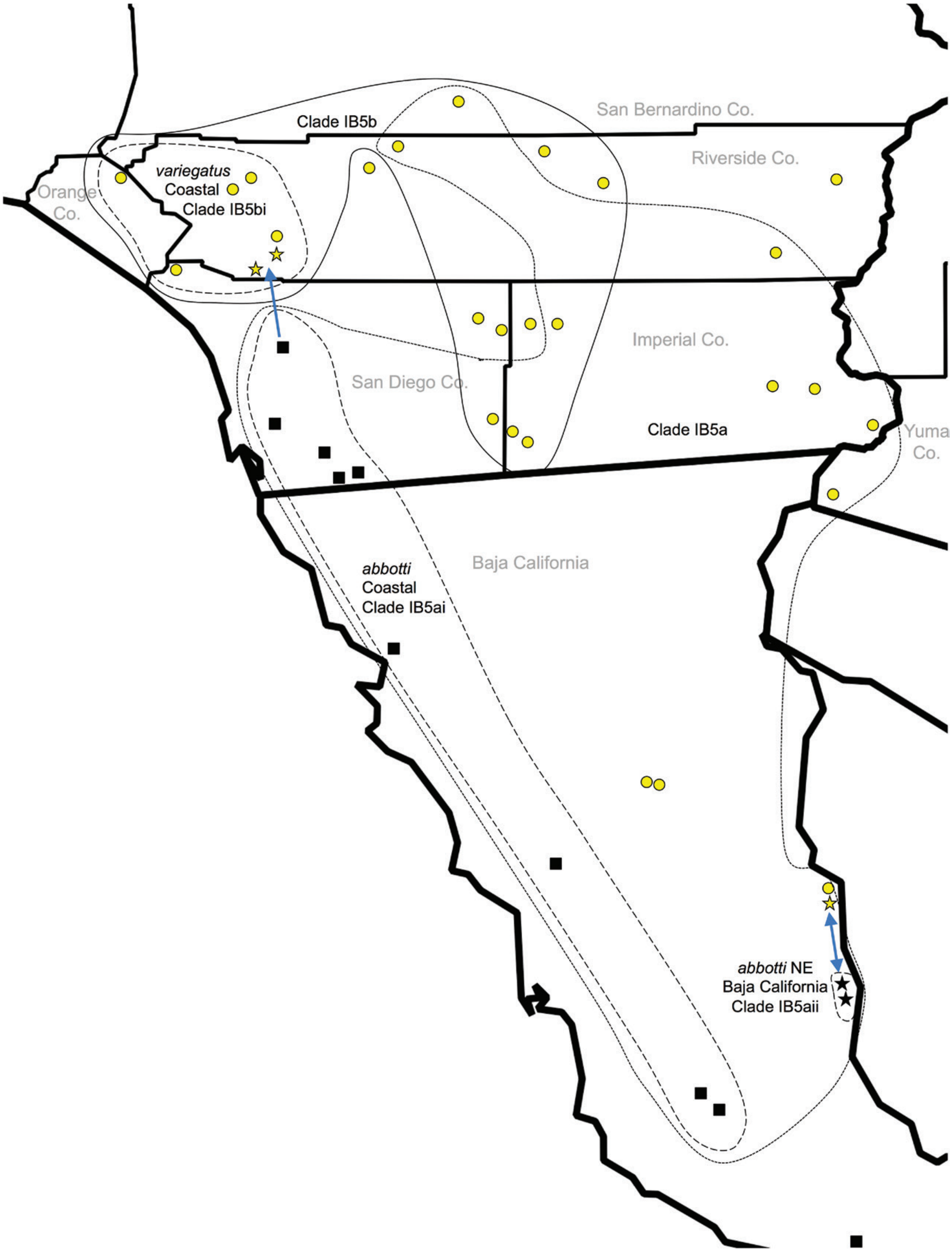

Figure 7. Distribution of mitochondrial lineages in southern California and northern Baja California, highlighting distributions of subclades IB5bi, IB5ai and IB5aii. Yellow circles indicate localities of sampled *C. v. variegatus*, black squares indicate *C. v. abbotti* localities. Nuclear introgression was detected at localities depicted with stars, and blue arrows indicate the direction of nuclear introgression.

both the continental *variegatus*- and peninsular *abbotti*-groups. Failure to account for introgression in the *BEAST analyses led to both reduced nodal support for the two clades as well as species tree compression in the crown age of *C. variegatus*. Given that post-divergence gene flow between sister-lineages (e.g. *C. v. variegatus* and *C. v. sonoriensis*) would not result in reduced nodal support, this destabilization in the topology (as inferred by reduced support values) is due to introgression between the non-sister-taxa *C. v. abbotti* and *C. v. variegatus*. The number of introgressed nuclear alleles at the *C. v. abbotti* and *C. v. variegatus* contact zone is not large relative to the entire dataset, only 0.5% (7 of 1300 alleles), yet this introgression still leads to distorted branch lengths and destabilization.

In addition to mito-nuclear discordance due to the geologically recent and easily detectable instances of introgression, we also infer two possible instances of ancient mitochondrial capture. The first hypothesized introgressive event has resulted in the original mtDNA genome of *C. v. abbotti* being completely lost and displaced by one 'captured' from the continental clade. Observed patterns in the nuclear loci bolster support for introgression rather than incomplete lineage sorting being the cause of mitochondrial non-monophyly of the peninsular group. Mitochondrial loci have, on average, an effective population size one fourth that of nuclear loci and hence are expected to coalesce more rapidly than nuclear loci. That three of the four nuclear loci recovered a monophyletic peninsular clade is suggestive that the mitochondrial gene tree would also have recovered a monophyletic peninsular clade were it not for introgression. While mitochondrial gene trees can often provide greater phylogenetic resolution relative to nuclear loci (Corl & Ellegren, 2013), a failure to account for introgressed genes in molecular phylogenies can lead to decreased support, decreased resolution and distortion in both topology and branch lengths during species tree inference (Near & Keck, 2013; Leaché *et al.*, 2014).

These data indicate that at least three distinct introgressive events from *C. v. variegatus* into *C. v. abbotti* led to the complete replacement of the native mitochondrial genome: mtDNA clade III is the oldest and first introgression that may have occurred during Late Pliocene or Early Pleistocene (2.38–3.16 Mya). The other two are more recent introgressive events, leading to the clades IB5ai and IB5aii, which occur in the northern distribution of *C. v. abbotti*. Clade IB5aii is restricted to the vicinity of Puertecitos, Baja California, while clade IB5ai is distributed over a large area in the southern California Floristic Province from at least Misión San Fernando Velicatá to north-central San Diego County, a linear distance of about 450 km. The pattern of repeated unidirectional mtDNA introgression among closely related species is not uncommon (Rapson *et al.*, 2012; Toews & Brelsford, 2012, Zieliński *et al.*, 2013) and can result from various processes (Roca *et al.*, 2005; Currat *et al.*, 2008; Toews *et al.*, 2014). For example, climate-induced distributional shifts may be responsible for an intriguing pattern of temporally separated and repeated mtDNA introgression from the lizard *Crotaphytus collaris* (Say, 1822) into the congener *C. bicinctores* Smith & Tanner, 1972 in western Arizona (McGuire *et al.*, 2007). Such studies suggest that the conditions responsible for introgression may persist for hundreds of thousands or millions of years.

The second instance of possible ancient mitochondrial capture relates to the widespread *C. v. variegatus* mtDNA clade I, which our analyses suggest originated via introgression with *C. v. sonoriensis*. While this introgressive event is less obvious, given the sister-relationship of *C. v. variegatus* and *C. v. sonoriensis*, both the modified BFD test of introgression and the gene-fitting with proportional branch lengths test support this inference. As with the introgressive event leading to mtDNA clade III, the mechanistic process responsible for the mtDNA capture leading to clade I is unknown. Both selection and distributional shifts may have played a role. The dated mtDNA gene tree indicates a crown age of 1.27 Mya (1.03–1.54 Mya) for clade I, which establishes the estimated youngest date for when this introgressive event occurred. Despite its large distribution over a topologically diverse landscape, the most recent common ancestor of this mtDNA clade is younger than that of clades III, IV and VI, which is suggestive that selection has played a role in determining its distribution (Bonnet *et al.*, 2017). The geologically young mitochondrial lineage IB4 also demonstrates cytonuclear discordance relative to nuclear boundaries between *C. v. variegatus* and *C. v. sonoriensis* in north-western Sonora. Multiple introgressive events are required to account for the recovered pattern, but whether this is the result of geologically recent bidirectional movement or repeated movement from *C. v. variegatus* back into *C. v. sonoriensis* can only be answered with additional sampling in this region.

In addition to mito-nuclear discordance resulting from introgression, a possible instance of incomplete lineage sorting causes additional discordance between the mitochondrial gene tree and nuclear-inferred species tree. This instance involves the mtDNA sister-clades IV and V within *C. v. variegatus* in the northern Mojave Desert (see Figs 2, 3). While the gene-fitting with proportional branch lengths analysis infers incomplete lineage sorting, the relative branch lengths of the mtDNA gene tree and the species tree do not demonstrate incomplete lineage sorting in the combined nDNA and mtDNA species tree analysis. Distinct boundaries among deeply divergent mitochondrial clades are observed in the northern Mojave region (clades I, IV and V), but these breaks are not accompanied by correspondingly deep differentiation with the nuclear data. The mitochondrial break between clades IA and IB matches up fairly well to the boundary between the Mojave and Colorado Deserts in southern California (see Fig. 3), but the nuclear data did not recover a corresponding break here. Other phylogeographic studies of lizards have recovered mitochondrial breaks that are not accompanied by deep nuclear differentiation (Ogden & Thorpe, 2002). Species whose dispersal distance is small relative to large geographic distributions may be more likely to show mtDNA patterns with a 'deeper time to monophyly' (Irwin, 2002), which can naturally lead to incomplete lineage sorting in a species tree (Patton & Smith, 1994). Sex-based differences in dispersal distances where females are more philopatric can also contribute to structured phylogeographic patterns in the mitochondrial gene tree that are incongruent with nuclear loci (Brandt *et al.*, 2012; Bidon *et al.*, 2014). On the other hand, other desert taxa harbour divergent mitochondrial lineages in the northern Mojave Desert (Graham *et al.*, 2015), as well as mitochondrial breaks near the Mojave/Colorado Desert boundary (Douglas *et al.*, 2006; Wood *et al.*, 2008b), which is suggestive of shared phylogeographic history. Given this possibility, a nuclear dataset that provides higher resolution than the one in this study may corroborate a vicariant origin of the deep mitochondrial structure observed.

BIOGEOGRAPHY AND TIMING OF DIVERSIFICATION

This study and others (e.g. Bastos-Silveira *et al.*, 2012) demonstrate that cytonuclear discordance can occur over a large geographic area thus obscuring biogeographic patterns. An interpretation of the mitochondrial data alone would have led to the mistaken conclusion that peninsular banded gecko populations had multiple, distinct origins. Biogeographic conclusions from previous studies that relied exclusively on mtDNA should undoubtedly be followed up with multilocus data (Bidon *et al.*, 2014). As previously mentioned, our combined analyses support Grismer's hypothesis that *C. variegatus* comprises distinct continental and peninsular groups.

While eublepharid geckos lack fossils suitable for molecular dating, the gekkotan mitochondrial substitution rate from Siler *et al.* (2012) results in age estimates compatible with our understanding of geomorphological history of the area and a hypothesized biogeographic model. This substitution rate (1.55% Myr^{-1}) is much faster than that estimated by Macey *et al.* (1999, 0.57% Myr^{-1}), and we recognize the need for further validation of this rate. The 1.55% Myr^{-1} mtDNA substitution rate (Siler *et al.*, 2012) was calculated using a secondary calibration from phylogenetic study of Gekkota (Gamble *et al.*, 2011). In our study, the divergence between *C. brevis* and *C. variegatus* is estimated at 14.75 Mya (10.22–18.88 Mya); this is somewhat younger than the ages estimated for this relationship in higher level studies (Gamble *et al.*, 2011, 2015), but not markedly so (e.g. confidence intervals are overlapping).

Our molecular dating analyses are also consistent with the aspect of Grismer's hypothesis that the principle geographic structure within *Coleonyx variegatus* is vicariant in origin via the formation of the northern Gulf of California. We estimated the divergence between the peninsular *abbotti*- and continental *variegatus*-groups to be 6.28 Mya (5.29–7.32 Mya). Grismer (1994) places northern gulf vicariance at 3 Mya, and Murphy (1983) used a similar time frame of 3–4 Mya for a similar vicariant event (formation of the 'San Gorgonio barrier'). Multiple molecular biogeographic studies have subsequently used this event in their models or as calibrations (e.g. Riddle *et al.*, 2000; Castoe *et al.*, 2007). More recent studies of geomorphological change in the region have firmly established that this time frame is too young. Dated sedimentary deposits near Santa Rosalía indicate that substantial marine incursions had extended to the central Gulf of California by ~7 Mya (Miller & Lizarralde, 2013). Various sedimentary deposits from San Gorgonio Pass in southern California to Isla Tiburón off the coast of Sonora, a distance of about 650 km, establish the subsequent synchronous development of a narrow marine incursion at approximately 6.3 Mya (McDougall *et al.*, 1999; Oskin & Stock, 2003a; Dorsey *et al.*, 2007; Bennett *et al.*, 2015; Umhoefer *et al.*, 2018). The geological evidence for the northern gulf formation and vicariance is thus consistent with our estimated divergence between the two *C. variegatus* groups. The Colorado River arrived at the northern Gulf of California at ~5.3 Mya (Dorsey *et al.*, 2007), carrying sediments that have filled the northern portion of the gulf. The resulting progradation of the Colorado River delta has pushed the head of the gulf further to the south, and by 4 Mya the northern gulf region was a subaerial delta plain, not marine (Winker & Kidwell, 1996; Dorsey, 2006, 2010), precluding the young age of the previously hypothesized northern vicariance. The progradation of the Colorado River delta is one of the two principle geological processes that have established terrestrial connectivity at the head of the gulf and brought the peninsular *C. v. abbotti* and continental *C. v. variegatus* into secondary contact; the second geological process is the northern movement of the Baja California peninsula relative to landmass opposite the San Andreas Fault. When the northern gulf formed, the Puertecitos region was proximate to the region in Sonora where Isla Tiburón is currently located, indicating a movement of ~235 km north-west (Oskin & Stock, 2003b; Bennett *et al.*, 2015).

While the northern gulf region transitioned from marine to terrestrial around 4 Mya, Plio-Pleistocene lakes in the Salton Trough, the marine Laguna Salada, and the Colorado River (e.g. Boehm, 1984) have also acted as intermittent barriers between the peninsular and continental fauna. Patterns of ancient introgression can inform historic biogeography (Spinks & Shaffer, 2009; Miller *et al.*, 2012; Pelser *et al.*, 2012), and in this instance, the estimated time-frame for the introgressive event that led to the replacement of the native *C. v. abbotti* mtDNA genome (estimated to be 2.38 to 3.13 Mya) corresponds with an increased opportunity for the previously isolated lineages to interact genetically.

While samples from the northern distribution of *C. v. peninsularis* are lacking from this study, the hypothesized distribution of *C. v. peninsularis* (Grismer, 2002), coupled with the recovered genetic break between *C. v. abbotti* and *C. v. peninsularis*, is suggestive of a coincident midpeninsular break seen in other taxa (Upton & Murphy, 1997; Riddle *et al.*, 2000; Zink, 2002; Lindell *et al.*, 2005; Crews & Hedin, 2006; Meik *et al.*, 2018). These midpeninsular genetic breaks have been posited to be the result of ephemeral marine seaways that bisected the peninsula. Dated marine sediments corroborating such seaways have yet to be discovered, and controversy about the existence, time frame, and possibility of multiple seaways remains (Murphy & Aguirre-León, 2002; Lindell *et al.*, 2006; Leaché *et al.*, 2007; Dolby *et al.*, 2015; Gottscho 2016). The earliest suggestion of a trans-peninsular seaway was by Cooper (1895), who invoked a geologically recent channel to explain the similarity of the molluscan fauna from the northern end of the Gulf of California with temperate Pacific regions at similar latitudes. The seaway invoked by Upton & Murphy (1997) was also geologically young (Pleistocene), but more recent investigations have entertained an idea of an older seaway in the Pliocene or Late Miocene (e.g. Lindell *et al.*, 2005). The divergence estimate between *C. v. abbotti* and *C. v. peninsularis* in our study is estimated to be about 4.2 Mya.

One of the prominent findings of this study is the inference of two independent range expansions into the Mediterranean climate of the California Floristic Province in coastal southern California and northern Baja California. The California Floristic Province (CFP) is a temperate biodiversity hotspot and contains numerous endemic species (Myers *et al.*, 2000). The immigration of many arid-adapted plant species into the region from southern deserts likely occurred geologically recently (Raven & Axelrod, 1978; Lancaster & Kay, 2013), perhaps as recently as the Xerothermic (8000–4000 years ago) (Axelrod, 1978). The genetically shallow mitochondrial divergences of coastal subclades IB5ai and IB5bi in this study suggests a time frame post-dating the last glacial maximum (LGM) for these range expansions. All five genetic markers indicate that the northern coastal expansion of *C. v. variegatus* (IB5bi) is derived from gecko populations of the Colorado Desert in southern California and south-western Arizona. The high elevations of the peninsular and transverse mountain ranges separate coastal gecko populations from desert populations to the east and north, and thus this northern dispersal must have entered coastal regions via a lower elevation pass; the San Gorgonio Pass between the San Jacinto Mountains and the San Bernardino Mountains to the north is a likely candidate route. While Klauber (1945) originally assigned these coastal populations to *C. v. abbotti*, he noted their morphological similarity to *C. v. variegatus* to the east and hypothesized intergradation. The coastal populations of *C. v. variegatus* can often retain the juvenile pattern into adulthood like *C. v. abbotti*, although they attain a larger adult size like their desert conspecifics. Whether the similarity in pattern is the result of convergence due to the shared environment in cooler coastal areas (Portik *et al.*, 2011) or due to introgression (e.g. Brockerville *et al.*, 2013) remains to be tested.

The second colonization of the California Floristic Province in coastal north-western Baja California and San Diego County, California (IB5ai) represents *C. v. abbotti* populations derived from the Peninsular Desert. This range expansion has resulted in *C. v. abbotti* carrying introgressed *C. v. variegatus*-mtDNA at least 450 km northward. Genetic studies of other taxa have revealed cytonuclear discordance over large geographical areas (Bastos-Silveira *et al.*, 2012), with range expansion following introgression being the evident mechanism (Neiva *et al.*, 2010). This geologically recent (post-LGM) distributional expansion into the California Floristic Province is likely a pattern for many other arid-adapted peninsular plants and animals. Zink (2002) suggested a recent northern dispersal of two bird species, and a cactus common to the coastal sage scrub community may have a recent hybrid origin from central Baja California coupled with a northern dispersal (Mayer *et al.*, 2000). Riddle and Hafner (2006) briefly discussed the possibility that a large proportion of widespread peninsular taxa may have shifted their distributions north and transformed ecological assemblages in the Peninsular North area. Genetic data supporting recent range expansions north into the CFP include species of snakes (Harrington *et al.*, 2018), lizards (McGuire *et al.*, 2007; Scott, 2013) and spiders (Crews & Hedin, 2006). Undoubtedly, further phylogeographic work of arid-adapted species of the southern California Floristic Province will reveal that their northern distribution results from post-LGM range expansions as well.

CONCLUSIONS

Baja California has become a model region for using multitaxa datasets to address the role of hypothesized vicariant events in lineage diversification. This study supports aspects of previous biogeographic models and adds an additional perspective to this system with the need to account for introgression in multilocus phylogeographic studies. Current technologies provide feasible approaches to generating multilocus datasets more representative of the entire genome, which will lead to better estimates of species boundaries, divergence times, and detection of post-divergence gene flow. This study also clarifies lineage boundaries of the San Diego banded gecko in southern California – a finding of conservation relevance as their known range within the United States is more restricted than previously believed.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Figure S1. Maximum likelihood inferred nuclear gene trees of the four nuclear loci (*BACH1, PRLR, R35, NKTR*) using RAxML.

Table S1. Primers used in PCR and sequencing reactions.

Appendix. Specimen information, including study ID, Genbank numbers, lineage membership, and locality.

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
BajaCalifornia01	MK944783/-/MK944928/ MK945109/ MK945327/ MK945537	abbotti	abbotti	IIIB	Baja California: Nuevo Rosarito, 2.2 km N of	28.65724	-114.0284
BajaCalifornia02	MK944758/MK944873/ MK944922/ MK945090/ MK945308/MK945518	abbotti	abbotti	IIIB	Baja California: Punta Prieta	28.92501	-114.16212
BajaCalifornia03	MK944524/-/-/-/-/-	abbotti	abbotti	IIIB	Baja California: Bahia de los Angeles	28.97967	-113.57733
BajaCalifornia04	MK944544/-/-/MK944963/ MK945181/MK945391	abbotti	abbotti	IIIB	Baja California: Bahia de los Angeles	28.97967	-113.57733
BajaCalifornia05	MK944593/-/MK944896/ MK944990/ MK945208/ MK945418	abbotti	abbotti	IIIB	Baja California: Bahia de los Angeles	28.97967	-113.57733
BajaCalifornia06	MK944749/MK944867/ MK944917/ MK945082/ MK945300/MK945510	abbotti	abbotti	IIIB	Baja California: Arroyo Rinconada	29.53049	-114.6524
BajaCalifornia07	MK944761/-/MK944925/ MK945093/ MK945311/ MK945521	abbotti	abbotti	IB5ai	Baja California: Mision San Fernando Velicata	29.97858	-115.23832
BajaCalifornia08	MK944794/-/-/MK945119/ MK945337/MK945547	abbotti	abbotti	IB5ai	Baja California: El Sauzalito	30.11322	-115.35454
BajaCalifornia09	MK944795/-/-/MK945120/ MK945338/MK945548	abbotti	abbotti	IB5ai	Baja California: El Sauzalito	30.11322	-115.35454
BajaCalifornia10	MK944796/-/-/-/-/-	abbotti	abbotti	IB5ai	Baja California: El Sauzalito	30.1145	-115.35483
BajaCalifornia11	MK944797/-/-/MK945121/ MK945339/MK945549	abbotti	abbotti	IB5ai	Baja California: San Telmo, 22.9 km E of	30.96512	-115.85193
BajaCalifornia12	MK944835/-/-/MK945142/ MK945360/MK945570	abbotti	abbotti	IB5ai	Baja California: Cañon Doña Petra, Ensenada	31.905	-116.6068
BajaCalifornia13	MK944771/-/-/MK945103/ MK945321/MK945531	abbotti Xvariegatus	abbotti	IB5aii	Baja California: Laguna Percubu, 46.7 km S of, on Mex Hwy 5	30.39794	-114.64329
BajaCalifornia14	MK944764/-/-/MK945096/ MK945314/MK945524	abbotti Xvariegatus	abbotti	IB5aii	Baja California: Laguna Percubu, 45.4 km S of, on Mex Hwy 5	30.41001	-114.64276
BajaCalifornia15	MK944770/-/-/MK945102/ MK945320/MK945530	abbotti Xvariegatus	abbotti	IB5aii	Baja California: Laguna Percubu, 43.5 km S of, on Mex Hwy 5	30.42651	-114.64664

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
BajaCalifornia16	MK944765/-/-/MK945097/ MK945315/MK945525	abbotti Xvariegatus	abbotti	IB5aii	Baja California: Laguna Percubu, 38.2 km S of, on Mex Hwy 5	30.47405	-114.66185
BajaCalifornia17	MK944772/-/-/MK945104/ MK945322/MK945532	abbotti Xvariegatus	abbotti	IB5aii	Baja California: Laguna Percubu, 36.4 km S of, on Mex Hwy 5	30.48984	-114.66687
BajaCaliforniaSur16	MK944821/MK944880/ MK944936/ MK945131/ MK945349/MK945559	abbotti Xpeninsularis	abbotti	IIIA	Baja California Sur: San Lucas, S Santa Rosalía, BCS	27.223	-112.221
BajaCaliforniaSur17	MK944542/MK944850/-/ MK944961/MK945179/ MK945389	abbotti Xpeninsularis	abbotti	IIIA	Baja California Sur: Tres Virgenes	27.43	-112.53
BajaCaliforniaSur18	MK944543/MK944851/-/ MK944962/MK945180/ MK945390	abbotti Xpeninsularis	abbotti	IIIA	Baja California Sur: Tres Virgenes	27.43	-112.53
BajaCaliforniaSur19	MK944750/MK944868/-/ MK945083/ MK945301/ MK945511	abbotti Xpeninsularis	abbotti	IIIA	Baja California Sur: Ejido Alfredo y Bonfil, 7.9 km NW of	27.42025	-112.75462
BajaCaliforniaSur20	MK944817/MK944881/ MK944934/ MK945127/ MK945345/MK945555	abbotti Xpeninsularis	abbotti	IIIB	Baja California Sur: Mesa Las Calabazas, Vizcaíno Desert, BCS	27.45933	-113.21568
BajaCaliforniaSur21	MK944820/MK944883/-/ MK945130/ MK945348/ MK945558	abbotti Xpeninsularis	abbotti	IIIB	Baja California Sur: Rancho Miramar (San Quintín, BCS)	28.15594	-113.61543
BajaCaliforniaSur22	MK944609/MK944857/-/ MK945005/ MK945223/ MK945433	abbotti	abbotti	IIIA	Baja California Sur: Punta Norte, Isla Cedros, Baja California	28.35682	-115.19568
BajaCaliforniaSur23	MK944610/MK944858/ MK944902/ MK945006/ MK945224/MK945434	abbotti	abbotti	IIIA	Baja California Sur: Punta Norte, Isla Cedros, Baja California	28.3533	-115.19509
SanDiego03	MK944842/-/-/MK945147/ MK945365/MK945575	abbotti	abbotti	IB5ai	California, San Diego Co.: San Pasqual	33.09471	-116.98417
SanDiego04	MK944843/-/-/MK945148/ MK945366/MK945576	abbotti	abbotti	IB5ai	California, San Diego Co.: San Pasqual	33.09157	-116.98619
SanDiego05	MK944845/-/-/MK945149/ MK945367/MK945577	abbotti	abbotti	IB5ai	California, San Diego Co.: San Pasqual	33.09965	-116.9736
SanDiego06	MK944846/-/MK944942/ MK945150/ MK945368/ MK945578	abbotti	abbotti	IB5ai	California, San Diego Co.: San Pasqual	33.09613	-116.98005

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
SanDiego07	MK944841/-/-/-/-/MK945583	abbotti	abbotti	IB5ai	California, San Diego Co.: San Pasqual	33.09965	-116.9736
SanDiego08	MK944844/-/-/-/-/MK945584	abbotti	abbotti	IB5ai	California, San Diego Co.: San Pasqual	33.09613	-116.98005
SanDiego09	MK944662/-/-/-/-/-	abbotti	abbotti	IB5ai	California, San Diego Co.: Marron Valley	32.59245	-116.76284
SanDiego10	MK944625/-/-/MK945017/ MK945235/MK945445	abbotti	abbotti	IB5ai	California, San Diego Co.: Hollenbeck Canyon	32.68946	-116.81755
SanDiego11	MK944626/-/-/-/-/MK945579	abbotti	abbotti	IB5ai	California, San Diego Co.: Hollenbeck Canyon	32.68946	-116.81755
SanDiego12	MK944627/-/-/-/-/MK945580	abbotti	abbotti	IB5ai	California, San Diego Co.: Hollenbeck Canyon	32.68946	-116.81755
SanDiego13	MK944628/-/-/MK945018/ MK945236/MK945446	abbotti	abbotti	IB5ai	California, San Diego Co.: Hollenbeck Canyon	32.68946	-116.81755
SanDiego14	MK944629/-/-/-/-/-	abbotti	abbotti	IB5ai	California, San Diego Co.: Hollenbeck Canyon	32.68946	-116.81755
SanDiego15	MK944607/-/-/MK945003/ MK945221/MK945431	abbotti	abbotti	IB5ai	California, San Diego Co.: Dulzura Summit	32.61779	-116.73463
SanDiego16	MK944838/MK944859/-/ MK945146/ MK945364/ MK945574	abbotti	abbotti	IB5ai	California, San Diego Co.: Barrett Lake Road	32.6167	-116.7
SanDiego17	MK944600/-/-/MK944994/ MK945212/MK945422	abbotti	abbotti	IB5ai	California, San Diego Co.: Mission Trails Regional Park	32.81575	-117.04269
SanDiego18	MK944833/-/-/MK945140/ MK945358/MK945568	abbotti	abbotti	IB5ai	California, San Diego Co.: Mission Trails Regional Park	32.81575	-117.04269
SanDiego19	MK944661/-/-/-/-/MK945581	abbotti	abbotti	IB5ai	California, San Diego Co.: Mission Trails Regional Park	32.81575	-117.04269
brevis10	MK944515/-/-/-/MK945369/-	brevis	brevis	brevis	unknown		
Brewster1	MK944516/-/-/MK944943/ MK945161/MK945371	brevis	brevis	brevis	Texas, Brewster Co.: BBNP, 'Black Knob'	29.196736	-103.027647
Otero1 TNHC61358	MK944519/-/-/MK944946/ MK945164/MK945374	brevis	brevis	brevis	New Mexico, Otero co.: Hwy 506, ~2 mi N Otero Co. Rd G5		
Presidio1 TNHC66997	MK944520/-/-/MK944947/ MK945165/MK945375	brevis	brevis	brevis	Texas, Presidio Co.: Fort Holland	30.54944	-104.66194

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Presidio2 TNHC66998	MK944521/MK944848/-/MK944948/MK945166/MK945376	brevis	brevis	brevis	Texas, Presidio Co.: Fort Holland	30.55	-104.66139
Presidio3 TNHC66999	MK944522/-/-/MK944949/MK945167/MK945377	brevis	brevis	brevis	Texas, Presidio Co.: Sierra Vieja Mts., Vieja Pass		
Presidio4 TNHC67347	MK944523/MK944849/MK944886/ MK944950/MK945168/MK945378	brevis	brevis	brevis	Texas, Presidio Co.: Sierra Vieja Mts., Box Canyon		
ValVerde1 TNHC53338	MK944517/MK944847/-/MK944944/MK945162/MK945372	brevis	brevis	brevis	Texas, Val Verde Co.: Langtry, .8 mi N on Pandale dirt road		
ValVerde2 TNHC58843	MK944518/-/-/MK944945/MK945163/MK945373	brevis	brevis	brevis	Texas, Val Verde Co.: Devils River State Natural Area, near bunkhouse		
ValVerde3	MK944514/-/-/-/-/-	brevis	brevis	brevis	Texas, Val Verde Co.: Pandale Road		
BajaCaliforniaSur03	MK944792/-/MK944931/MK945117/ MK945335/MK945545	peninsularis	peninsularis	VIA	Baja California Sur: San Juan de Los Planes, 4.2 km S of	23.93697	-109.97251
BajaCaliforniaSur01	MK944784/MK944876/MK944929/ MK945110/MK945328/MK945538	peninsularis	peninsularis	VIA	Baja California Sur: Los Barriles, 5.4 km N of	23.72522	-109.71966
BajaCaliforniaSur02	MK944791/-/-/MK945116/MK945334/MK945544	peninsularis	peninsularis	VIA	Baja California Sur: Los Barriles, 7.2 km N of	23.74623	-109.72331
BajaCaliforniaSur04	MK944788/-/-/MK945114/MK945332/MK945542	peninsularis	peninsularis	VIB	Baja California Sur: Meliton Albañez Dominguez, 14.3 km E of	23.64031	-110.28924
BajaCaliforniaSur05	MK944789/-/-/-/-/-	peninsularis	peninsularis	VIB	Baja California Sur: Meliton Albañez Dominguez, 3.4 km E of	23.65104	-110.39729
BajaCaliforniaSur06	MK944790/-/-/MK945115/MK945333/MK945543	peninsularis	peninsularis	VIB	Baja California Sur: Meliton Albañez Dominguez, 12.2 km E of	23.63647	-110.31316
BajaCaliforniaSur07	MK944785/-/MK944930/MK945111/ MK945329/MK945539	peninsularis	peninsularis	VIB	Baja California Sur: El Centenario, 5.1 km NW of	24.13679	-110.4669
BajaCaliforniaSur08	MK944786/-/-/MK945112/MK945330/MK945540	peninsularis	peninsularis	VIB	Baja California Sur: El Centenario, 6.5 km NW of	24.14318	-110.47908

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
BajaCaliforniaSur09	MK944787/-/-/MK945113/ MK945331/MK945541	peninsularis	peninsularis	VIB	Baja California Sur: El Centenario, 16.1 km NW of	24.19427	-110.55618
BajaCaliforniaSur10	MK944819/MK944882/-/ MK945129/ MK945347/ MK945557	peninsularis	peninsularis	VIB	Baja California Sur: 36 km N La Paz, BCS	24.10069	-110.73183
BajaCaliforniaSur11	MK944762/MK944875/ MK944926/ MK945094/ MK945312/MK945522	peninsularis	peninsularis	VIB	Baja California Sur: Ley Federal Agraria Dos, 14.1 km NE of	24.11491	-110.75033
BajaCaliforniaSur12	MK944608/MK944856/-/ MK945004/ MK945222/ MK945432	peninsularis	peninsularis	VIB	Baja California Sur: Isla Santa Margarita	24.50175	-111.84953
BajaCaliforniaSur13	MK944759/MK944874/ MK944923/ MK945091/ MK945309/MK945519	peninsularis	peninsularis	VIB	Baja California Sur: Isla Santa Margarita	24.45392	-111.77314
BajaCaliforniaSur14	MK944527/-/-/MK944952/ MK945170/MK945380	peninsularis	peninsularis	VIB	Baja California Sur: El Bosque 3	24.79922	-110.84235
BajaCaliforniaSur15	MK944793/MK944877/ MK944932/ MK945118/ MK945336/MK945546	peninsularis	peninsularis	VIB	Baja California Sur: Los Dolores	25.07882	-110.8622
Sonora01 MVZ144191	MK944663/-/MK944904/ MK945030/ MK945248/ MK945458	sonoriensis	sonoriensis	II	Sonora: 4 mi E Bahia de Kino on Mx Hwy 16	28.828958	-111.882131
Sonora02 MVZ144192	MK944664/-/MK944905/ MK945031/ MK945249/ MK945459	sonoriensis	sonoriensis	II	Sonora: 4 mi E Bahia de Kino on Mx Hwy 16	28.828958	-111.882131
Sonora03	MK944756/MK944871/ MK944920/ MK945088/ MK945306/MK945516	sonoriensis	sonoriensis	II	Sonora: Puerto Libertad, 128.7 km SE of (on Son Hwy 29)	29.15857	-111.71731
Sonora04	MK944753/MK944869/ MK944918/ MK945085/ MK945303/MK945513	sonoriensis	sonoriensis	II	Sonora: Puerto Libertad, 44.4 km SSE of (on Son Hwy 29)	29.65968	-112.31876
Sonora05	MK944836/-/-/MK945143/ MK945361/MK945571	sonoriensis	sonoriensis	II	Sonora: Las Haciendas, Real del Alamito, by Hermosillo	29.24541	-110.84034
Sonora06	MK944837/-/-/MK945160/-/ MK945582	sonoriensis	sonoriensis	II	Sonora: Valle Del Torreon, Real del Alamito, by Hermosillo	29.25495	-110.86257

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Sonora07	MK944630/-/MK944941/ MK945144/ MK945362/ MK945572	sonoriensis	sonoriensis	II	Sonora: Valle Del Torreon, Real del Alamito, by Hermosillo	29.25456	-110.86324
Sonora08	MK944631/-/-/MK945145/ MK945363/MK945573	sonoriensis	sonoriensis	II	Sonora: Las Haciendas, Real del Alamito, by Hermosillo	29.24007	-110.82819
Sonora09	MK944757/MK944872/ MK944921/ MK945089/ MK945307/MK945517	sonoriensis	sonoriensis	IB4	Sonora: Caborca; Jct Sonoran Hwys 44 & 21, 24.2 km S of (on Son Hwy 21)	30.53998	-112.29613
Sonora10	MK944754/MK944870/ MK944919/ MK945086/ MK945304/MK945514	sonoriensis	sonoriensis	IB4	Sonora: Caborca; Jct Sonoran Hwys 44 & 21, 1.2 km S of (on Son Hwy 21)	30.69299	-112.20546
Sonora11	MK944755/-/-/MK945087/ MK945305/MK945515	sonoriensis	sonoriensis	IB4	Sonora: Caborca; Jct Sonoran Hwys 44 & 21, 1.1 km S of (on Son Hwy 21)	30.69333	-112.2056
Animas1	MK944526/-/-/MK944951/ MK945169/MK945379	bogerti	variegatus	IB3	New Mexico, Animans Co.: Antelope Pass	31.94395	-108.92685
BajaCalifornia18	MK944769/-/-/MK945101/ MK945319/MK945529	variegatus	variegatus	IB5	Baja California: Laguna Percubu, 3.6 km W of	30.81653	-114.74263
BajaCalifornia19	MK944766/-/-/MK945098/ MK945316/MK945526	variegatus	variegatus	IB5	Baja California: Laguna Percubu, 7.7 km NNW of, on Mex Hwy 5	30.88073	-114.73366
BajaCalifornia20	MK944767/-/-/MK945099/ MK945317/MK945527	variegatus	variegatus	IB5	Baja California: Laguna Percubu, 9.8 km N of, on Mex Hwy 5	30.90211	-114.72666
BajaCalifornia21	MK944768/-/-/MK945100/ MK945318/MK945528	variegatus	variegatus	IB5	Baja California: San Felipe, 19.7 km SSE of, on Mex Hwy 5	30.91692	-114.72009
BajaCalifornia22	MK944776/-/-/MK945105/ MK945323/MK945533	variegatus	variegatus	IB5	Baja California: San Matias, 19.2 km SE of, on Mex Hwy 3	31.28698	-115.35046
BajaCalifornia23	MK944763/-/-/MK945095/ MK945313/MK945523	variegatus	variegatus	IB5	Baja California: San Matias, 18.1 km SE of, on Mex Hwy 3	31.28934	-115.36187
BajaCalifornia24	MK944782/-/-/MK945108/ MK945326/MK945536	variegatus	variegatus	IB5	Baja California: San Matias, 17.5 km SE of, on Mex Hwy 3	31.29055	-115.36785

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
BajaCalifornia25	MK944780/-/MK944927/ MK945106/ MK945324/ MK945534	variegatus	variegatus	IB5	Baja California: San Matias, 17.4 km SE of, on Mex Hwy 3	31.29066	-115.36854
BajaCalifornia26	MK944773/-/-/-/-/-	variegatus	variegatus	IB5	Baja California: San Matias, 16.3 km SE of, on Mex Hwy 3	31.29305	-115.38046
BajaCalifornia27	MK944781/-/-/MK945107/ MK945325/MK945535	variegatus	variegatus	IB5	Baja California: San Matias, 16.3 km SE of, on Mex Hwy 3	31.29301	-115.37998
BajaCalifornia28	MK944774/-/-/-/-/-	variegatus	variegatus	IB5	Baja California: San Matias, 14.9 km SE of, on Mex Hwy 3	31.296	-115.39457
BajaCalifornia29	MK944775/-/-/-/-/-	variegatus	variegatus	IB5	Baja California: San Matias, 12.1 km SE of, on Mex Hwy 3	31.30072	-115.42252
BajaCalifornia30	MK944777/-/-/-/-/-	variegatus	variegatus	IB5	Baja California: San Matias, 12.1 km SE of, on Mex Hwy 3	31.30083	-115.42286
BajaCalifornia31	MK944778/-/-/-/-/-	variegatus	variegatus	IB5	Baja California: San Matias, 11.2 km SE of, on Mex Hwy 3	31.30305	-115.43203
BajaCalifornia32	MK944779/-/-/-/-/-	variegatus	variegatus	IB5	Baja California: San Matias, 12.0 km SE of, on Mex Hwy 3	31.30093	-115.42426
Clark01	MK944717/-/-/MK945064/ MK945282/MK945492	utahensis	variegatus	IVB	Nevada, Clark Co.: Duck Hunters Mothers, Virgin River, 7.2 mi (airline) NE Overton	36.59477	-114.3363
Clark02	MK944718/-/-/MK945065/ MK945283/MK945493	utahensis	variegatus	IVB	Nevada, Clark Co.: Duck Hunters Mothers, Virgin River, 7.2 mi (airline) NE Overton	36.59477	-114.3363
Clark03	MK944615/-/-/MK945011/ MK945229/MK945439	utahensis	variegatus	IVB	Nevada, Clark Co.: Lake Mead	36.22968	-114.6083
Clark04	MK944675/-/-/MK945040/ MK945258/MK945468	utahensis	variegatus	IVB	Nevada, Clark Co.: Lake Mead	36.22694	-114.61837
Clark05	MK944614/-/-/MK945010/ MK945228/MK945438	utahensis	variegatus	IVB	Nevada, Clark Co.: Lake Mead	36.21226	-114.64933

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Clark06	MK944676/-/-/MK945041/ MK945259/MK945469	utahensis Xvariegatus	variegatus	IVB	Nevada, Clark Co.: Lake Mead	36.18196	-114.75652
Clark07	MK944613/-/-/MK945009/ MK945227/MK945437	utahensis Xvariegatus	variegatus	IVB	Nevada, Clark Co.: Lake Mead	36.12137	-114.90502
Clark08	MK944677/-/-/MK945042/ MK945260/MK945470	utahensis Xvariegatus	variegatus	IVB	Nevada, Clark Co.: Lake Mead	36.19812	-114.93182
Clark09	MK944624/-/-/MK945016/ MK945234/MK945444	variegatus	variegatus	IA	Nevada, Clark Co.: East of Searchlight	35.48188	-114.76037
Clark10	MK944596/-/-/-/-/-	variegatus	variegatus	IVB	Nevada, Clark Co.: Hwy 156 Lee Canyon Road	36.4674	-115.47952
Cochise1	MK944562/-/-/MK944968/ MK945186/MK945396	bogerti	variegatus	IB3	Arizona, Cochise Co.: W of San Simon	32.2753	-109.24518
Cochise2	MK944595/-/-/-/-/-	bogerti	variegatus	IB3	Arizona, Coshise Co.: Benson	31.98934	-110.30986
Coconino1	MK944825/MK944885/ MK944938/ MK945134/ MK945352/MK945562	utahensis	variegatus	IVA	Arizona, Coconino Co.: Deadman Wash, Wupatki NM	35.5347	-111.34261
Gila1 MVZ161445	AB114446/ AB114446/-/-/-/-	bogerti Xvariegatus	variegatus	IB1	Arizona, Gila Co.: SW Salt River Mts.	33.5717	-110.9267
Gila2 MVZ161446	MK944665/-/-/MK945032/ MK945250/MK945460	bogerti Xvariegatus	variegatus	IB3	Arizona, Gila Co.: SW Salt River Mts.	33.5717	-110.9267
Gila3 MVZ161447	MK944666/-/MK944906/ MK945033/ MK945251/ MK945461	bogerti Xvariegatus	variegatus	IB3	Arizona, Gila Co.: SW Salt River Mts.	33.5717	-110.9267
Gila4	MK944826/-/-/-/-/-	bogerti Xvariegatus	variegatus	IB3	Arizona, Gila Co.: Theodore Roosevelt Lake	33.74267	-111.22783
Gila5 MVZ232580	MK944667/-/MK944907/ MK945034/ MK945252/ MK945462	bogerti Xvariegatus	variegatus	IB3	Arizona, Gila Co.: 6.5 km SE by air of Roosevelt	33.62733	-111.102
Gila6 MVZ232581	MK944668/-/-/MK945035/ MK945253/MK945463	bogerti Xvariegatus	variegatus	IB3	Arizona, Gila Co.: 6.5 km SE by air of Roosevelt	33.62733	-111.102
Gila7	MK944710/-/-/MK945059/ MK945277/MK945487	bogerti Xvariegatus	variegatus	IB3	Arizona, Gila Co.: S of Pinal Mts., Cedar Creek, 1.4 mi SE Government Springs	33.23675	-110.9371
Gila8	MK944547/-/-/-/-/-	bogerti Xvariegatus	variegatus	IB3	Arizona, Gila Co.: Apache Trail	33.5526	-110.9483
Graham1	MK944705/-/-/MK945056/ MK945274/MK945484	bogerti	variegatus	IB3	Arizona, Graham Co.: 7.9 mi N Gila River at Fort Thomas	33.142	-109.93568

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Graham2	MK944706/-/MK944911/ MK945057/ MK945275/ MK945485	bogerti	variegatus	IB3	Arizona, Graham Co.: 7.9 mi N Gila River at Fort Thomas	33.142	-109.93568
Graham3	MK944707/-/-/MK945058/ MK945276/MK945486	bogerti	variegatus	IB3	Arizona, Graham Co.: 7.9 mi N Gila River at Fort Thomas	33.142	-109.93568
Greenlee1	MK944712/MK944862/ MK944912/ MK945061/ MK945279/MK945489	bogerti	variegatus	IB3	Arizona, Graham Co.: Eagle Creek, 8.9 mi (airline) W Clifton	33.0683	-109.44987
Imperial01	MK944545/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Laguna Dam	32.825	-114.4958
Imperial02	MK944546/-/-/-/-/-	variegatus	variegatus	IB1	California, Imperial Co.: Laguna Dam	32.82738	-114.49905
Imperial03	MK944760/-/MK944924/ MK945092/ MK945310/ MK945520	variegatus	variegatus	IB5	California, Imperial Co.: Ogilby Rd. N of I-8	32.95377	-114.89423
Imperial04	MK944724/-/-/MK945070/ MK945288/MK945498	variegatus	variegatus	IB5	California, Imperial Co.: Algodones Dunes	32.9716	-115.18615
Imperial05	MK944744/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Salton Sea	33.19648	-115.84783
Imperial06	MK944745/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Salton Sea	33.19648	-115.84783
Imperial07	MK944746/-/-/MK945080/ MK945298/MK945508	variegatus	variegatus	IB5	California, Imperial Co.: Salton Sea	33.19648	-115.84783
Imperial08	MK944747/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Salton Sea	33.19648	-115.84783
Imperial09	MK944748/-/-/MK945081/ MK945299/MK945509	variegatus	variegatus	IB5	California, Imperial Co.: Salton Sea	33.19648	-115.84783
Imperial10	MK944561/-/-/MK944967/ MK945185/MK945395	variegatus	variegatus	IB5	California, Imperial Co.: Tule Wash	33.19411	-116.00926
Imperial11	MK944798/MK944878/ MK944933/ MK945122/ MK945340/MK945550	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 10.1 km NW of on S2	32.78674	-116.1
Imperial12	MK944799/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 10.1 km NW of on S2	32.78674	-116.1

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Imperial13	MK944800/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 7.3 km NW of on S2	32.76888	-116.07677
Imperial14	MK944801/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 7.2 km NW of on S2	32.76798	-116.07561
Imperial15	MK944802/-/-/MK945123/ MK945341/MK945551	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 4.6 km NW of on S2	32.75455	-116.05128
Imperial16	MK944803/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 4.6 km NW of on S2	32.75455	-116.05128
Imperial17	MK944804/MK944879/-/ MK945124/ MK945342/ MK945552	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 4.6 km NW of on S2	32.75455	-116.05128
Imperial18	MK944805/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 3.9 km NW of on S2	32.75243	-116.04421
Imperial19	MK944806/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 3.9 km NW of on S2	32.75243	-116.04421
Imperial20	MK944807/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 2.3 km W of on S2	32.74727	-116.02708
Imperial21	MK944808/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 7.1 km NW of on S2	32.76737	-116.07475
Imperial22	MK944809/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 8.5 km NW of on S2	32.77034	-116.08759
Imperial23	MK944810/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 5.2 km NW of on S2	32.772	-116.04822
Imperial24	MK944811/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, .5 km W of on S2	32.74268	-116.00688
Imperial25	MK944812/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 5.5 km NW of on S2	32.75666	-116.05842

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Imperial26	MK944813/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 2.7 km N of on Shell Cyn Rd	32.77133	-116.00344
Imperial27	MK944814/-/-/MK945125/ MK945343/MK945553	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 4.9 km NW of on S2	32.75476	-116.0582
Imperial28	MK944815/-/-/MK945126/ MK945344/MK945554	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 8.6 km NW of on S2	32.7811	-116.08433
Imperial29	MK944816/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: Ocotillo, 8.6 km NW of on S2	32.7811	-116.08433
Imperial30	MK944832/-/-/-/-/-	variegatus	variegatus	IB5	California, Imperial Co.: S2 near Ocotillo	32.75257	-116.04497
Inyo01	MK944582/MK944854/ MK944893/ MK944981/ MK945199/MK945409	variegatus	variegatus	V	California, Inyo Co.: Homewood Canyon	35.89182	-117.3559
Inyo02	MK944583/-/-/MK944982/ MK945200/MK945410	variegatus	variegatus	V	California, Inyo Co.: NE Big Pine	37.2188	-118.23061
Inyo03	MK944584/-/-/MK944983/ MK945201/MK945411	variegatus	variegatus	V	California, Inyo Co.: NE Big Pine	37.19391	-118.24865
Inyo04	MK944585/-/MK944894/ MK944984/ MK945202/ MK945412	variegatus	variegatus	V	California, Inyo Co.: NE Big Pine	37.16833	-118.19387
Inyo05	MK944586/MK944855/-/ MK944985/ MK945203/ MK945413	variegatus	variegatus	V	California, Inyo Co.: N Eureka Valley	37.28288	-117.90877
Inyo06	MK944587/-/-/MK944986/ MK945204/MK945414	variegatus	variegatus	V	California, Inyo Co.: N Eureka Valley	37.25765	-117.92852
Inyo07	MK944588/-/MK944895/ MK944987/ MK945205/ MK945415	variegatus	variegatus	V	California, Inyo Co.: Last Chance Range	37.22734	-117.71819
Inyo08	MK944589/-/-/MK944988/ MK945206/MK945416	variegatus	variegatus	V	California, Inyo Co.: Last Chance Range	37.21502	-117.69812
Inyo09	MK944611/-/-/MK945007/ MK945225/MK945435	variegatus	variegatus	V	California, Inyo Co.: Scottys Castle	37.02834	-117.34251

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Inyo10	MK944612/-/MK944903/ MK945008/ MK945226/ MK945436	variegatus	variegatus	V	California, Inyo Co.: Scottys Castle	37.03215	-117.32422
Inyo11	MK944548/-/MK944899/ MK944995/ MK945213/ MK945423	variegatus	variegatus	V	California, Inyo Co.: vic. Darwin Falls	36.34	-117.511
Inyo12	MK944840/-/-/-/-/-	variegatus	variegatus	V	California, Inyo Co.: vic. Darwin Falls	36.34	-117.511
Kern1	MK944605/-/-/MK945001/ MK945219/MK945429	variegatus	variegatus	IA	California, Kern Co.: Dove Springs	35.41361	-118.03209
Kern2	MK944606/-/MK944901/ MK945002/ MK945220/ MK945430	variegatus	variegatus	IA	California, Kern Co.: Dove Springs	35.41047	-118.02708
LaPaz1	MK944592/-/-/MK944989/ MK945207/MK945417	variegatus	variegatus	IB1	Arizona, La Paz Co.: Wenden	33.86408	-113.54406
LaPaz2	MK944575/MK944853/-/ MK944976/MK945194/ MK945404	variegatus	variegatus	IB1	Arizona, La Paz Co.: Hwy. 95 south of Quartzite	33.56642	-114.21714
LaPaz3	MK944831/-/MK944940/ MK945139/ MK945357/ MK945567	variegatus	variegatus	IB1	Arizona, La Paz Co.: Hwy 95	33.5225	-114.2215
LaPaz4	MK944576/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, La Paz Co.: Hwy. 95 south of Quartzite	33.43091	-114.21689
LaPaz5	MK944577/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, La Paz Co.: Hwy. 95 south of Quartzite	33.33432	-114.21716
LaPaz6	MK944563/-/-/MK944969/ MK945187/MK945397	variegatus	variegatus	IB1	Arizona, La Paz Co.: Hwy. 95, S of I-10	33.33176	-114.21705
LaPaz7	MK944564/-/-/ MK944970/ MK945188/MK945398	variegatus	variegatus	IB1	Arizona, La Paz Co.: Hwy. 95, S of I-10	33.21792	-114.26013
LaPaz8	MK944534/-/-/ MK944955/ MK945173/MK945383	variegatus	variegatus	IB1	Arizona, La Paz Co.: S. of I-10 vic. little Harquahala Mts.	33.591	-113.584
LaPaz9	MK944535/-/-/ MK944956/ MK945174/MK945384	variegatus	variegatus	IB1	Arizona, La Paz Co.: S. of I-10 vic. little Harquahala Mts.	33.591	-113.584
LosAngeles1	MK944743/-/MK944916/ MK945079/ MK945297/ MK945507	variegatus	variegatus	IA	California, Los Angeles Co.: Pearblossom, Longview Road N of Pearblossom	34.55015	-117.89032

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Maricopa01	MK944552/MK944852/-/-/-/-	variegatus	variegatus	IB2	Arizona, Maricopa Co.: Salome Rd, 1.5 mi W of Jct with Eagle Eye Road	33.61636	-113.31591
Maricopa02	MK944551/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, Maricopa Co.: 20.6 mi S of Cattle Crossing, Eagle Eye Rd	33.6315	-113.30053
Maricopa03	MK944550/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, Maricopa Co.: 10.6 mi S of Cattle Crossing, Eagle Eye Rd	33.75199	-113.26576
Maricopa04	MK944590/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, Maricopa Co.: Painted Rock Road	32.97731	-112.98945
Maricopa05	MK944566/-/MK944890/ MK944972/ MK945190/ MK945400	variegatus	variegatus	IB1	Arizona, Maricopa Co.: Hwy. 85	33.13486	-112.65069
Maricopa06	MK944828/-/-/MK945136/ MK945354/MK945564	variegatus	variegatus	IB3	Arizona, Maricopa Co.: 7.9 mi S I-8 exit 144 Vekol Rd.	32.73733	-112.23267
Maricopa07	MK944604/-/-/MK945159/-/-	variegatus	variegatus	IB3	Arizona, Maricopa Co.: Scottsdale	33.672179	-111.877679
Maricopa08	MK944692/-/-/MK945047/ MK945265/MK945475	variegatus	variegatus	IB1	Arizona, Maricopa Co.: 2.5 mi (rd) NE Mobile	33.06574	-112.23049
Maricopa09	MK944694/-/-/MK945049/ MK945267/MK945477	variegatus	variegatus	IB1	Arizona, Maricopa Co.: vic. Of Mobile	33.06733	-112.26917
Maricopa10	MK944695/-/-/-/MK945370/-	variegatus	variegatus	IB1	Arizona, Maricopa Co.: vic. Of Mobile	33.06733	-112.26917
Maricopa11	MK944696/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, Maricopa Co.: vic. Of Mobile	33.06733	-112.26917
Maricopa12	MK944699/-/-/-/-/-	variegatus	variegatus	IB3	Arizona, Maricopa Co.: Vekol Valley, Vekol Rd at I-8	32.84547	-112.25597
Maricopa13	MK944700/-/-/MK945051/ MK945269/MK945479	variegatus	variegatus	IB1	Arizona, Maricopa Co.: Vekol Valley, Vekol Rd at I-8	32.84547	-112.25597
Maricopa14	MK944567/-/-/-/-/-	variegatus	variegatus	IB3	Arizona, Maricopa Co.: S of Sunflower	33.7938	-111.5257
Maricopa15	MK944568/-/-/-/-/-	variegatus	variegatus	IB3	Arizona, Maricopa Co.: S of Sunflower	33.7938	-111.5257
Maricopa16	MK944569/-/-/-/-/-	variegatus	variegatus	IB3	Arizona, Maricopa Co.: S of Sunflower	33.7938	-111.5257

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Maricopa17 MVZ232582	MK944669/-/-/MK945036/ MK945254/MK945464	variegatus	variegatus	IB3	Arizona, Maricopa Co.: 5.6 km S(via Hwy 87) of Sunflower	33.82467	-111.47583
Maricopa18 MVZ232583	MK944670/-/-/MK945037/ MK945255/MK945465	variegatus	variegatus	IB3	Arizona, Maricopa Co.: 5.6 km S(via Hwy 87) of Sunflower	33.82467	-111.47583
Maricopa19 MVZ232584	MK944673/-/-/-/-/-	variegatus	variegatus	IB3	Arizona, Maricopa Co.: 5.6 km S(via Hwy 87) of Sunflower	33.82467	-111.47583
Maricopa20 MVZ232585	MK944671/-/-/-/-/-	variegatus	variegatus	IB3	Arizona, Maricopa Co.: 5.6 km S(via Hwy 87) of Sunflower	33.82467	-111.47583
Mohave1	MK944644/-/-/-/-/-	variegatus	variegatus	IVB	Arizona, Mohave Co.: S of Wikieup	34.60643	-113.4872
Mohave2	MK944702/MK944861/ MK944909/ MK945053/ MK945271/MK945481	variegatus	variegatus	IVB	Arizona, Mohave Co.: Vicinity of Lower Tom Brown Well, 7.9 mi E Big Sandy River by road	34.91767	-113.515
Mohave3	MK944703/-/-/MK945054/ MK945272/MK945482	variegatus	variegatus	IVB	Arizona, Mohave Co.: Vicinity of Lower Tom Brown Well, 7.9 mi (rd) E Big Sandy River	34.91767	-113.515
Mohave4	MK944719/MK944863/ MK944914/ MK945066/ MK945284/MK945494	utahensis	variegatus	IVB	Arizona, Mohave Co.: Upper Hurricane Valley, 4.7 mi north by northwest of Mt. Trumbull School House	36.47712	-113.34782
Mohave5	MK944721/-/-/MK945067/ MK945285/MK945495	utahensis	variegatus	IVB	Arizona, Mohave Co.: tank at Jacobs Ranch, 2.8 mi (airline) ENE Whitney Pass	36.54232	-114.0193
Mohave6	MK944594/-/-/-/-/-	utahensis	variegatus	IVA	Arizona, Mohave Co.: Blackrock Road	36.9937	-113.6494
Nye1	MK944597/-/MK944897/ MK944991/ MK945209/ MK945419	variegatus	variegatus	IA	Nevada, Nye Co.: Amargosa Valley	36.61647	-116.54297
Orange1	MK944727/-/-/MK945071/ MK945289/MK945499	abbotti	variegatus	IB5bi	California, Orange Co.: Chino Hills State Park	33.859	-117.68457

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Pima01	MK944827/-/MK944939/ MK945135/ MK945353/ MK945563	variegatus	variegatus	IB1	Arizona, Pima Co.: 3 miles N of Ajo on Hwy. 85	32.45317	-112.87133
Pima02 ROM43696	MK944734/-/-/MK945075/ MK945293/MK945503	variegatus	variegatus	IB1	Arizona, Pima Co.: Gila Bend, 9.4 miles south on Hwy 85	32.844423	-112.7719116
Pima03 ROM43697	MK944735/-/-/MK945076/ MK945294/MK945504	variegatus	variegatus	IB1	Arizona, Pima Co.: Ajo, 6.8 miles north on Hwy 85 toward Gila Bend	32.48833	-112.88109
Pima04 ROM43700	MK944736/-/-/MK945077/ MK945295/MK945505	variegatus	variegatus	IB1	Arizona, Pima Co.: Ajo, 6.8 miles north on Hwy 85 toward Gila Bend	32.48833	-112.88109
Pima05 ROM43701	MK944737/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, Pima Co.: Gila Bend, 19.3 miles south on Hwy 85	32.68422	-112.85512
Pima06 ROM43702	MK944738/-/-/MK945078/ MK945296/MK945506	variegatus	variegatus	IB1	Arizona, Pima Co.: Gila Bend, 4.6 miles south on Hwy 85	32.8899663	-112.7499389
Pima07 ROM43703	MK944739/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, Pima Co.: Ajo, 3.4 miles north on Hwy 85 toward Gila Bend	32.43983	-112.87133
Pima08 ROM43704	MK944740/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, Pima Co.: Ajo, 9.2 miles north on Hwy 85 toward Gila Bend	32.5246	-112.8803
Pima09 ROM43705	MK944741/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, Pima Co.: Gila Bend, 11.9 miles south on Hwy 85	32.77676	-112.81167
Pima10 ROM43706	MK944742/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, Pima Co.: Gila Bend, 14 miles south on Hwy 85	32.75192	-112.82513
Pima11	MK944591/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, Pima Co.: Ajo	32.3395	-112.84971
Pima12	MK944701/-/-/MK945052/ MK945270/MK945480	bogerti	variegatus	IB3	Arizona, Pima Co.: Avra Valley	32.44491	-111.30426
Pima13	MK944571/-/-/-/-/-	bogerti	variegatus	IB3	Arizona, Pima Co.: Avra Valley Road	32.37505	-111.36229
Pima14	MK944573/-/-/-/-/-	bogerti	variegatus	IB3	Arizona, Pima Co.: Avra Valley Road	32.37108	-111.37739

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Pima15	MK944572/-/-/ MK944974/ MK945192/MK945402	bogerti	variegatus	IB3	Arizona, Pima Co.: Sonoran Desert Museum	32.23632	-111.16989
Pima16	MK944574/-/-/ MK944975/ MK945193/MK945403	bogerti	variegatus	IB3	Arizona, Pima Co.: Sonoran Desert Museum	32.22192	-111.16192
Pima17	MK944722/-/-/MK945068/ MK945286/MK945496	bogerti	variegatus	IB3	Arizona, Pima Co.: Altar Valley, 0.6 mi (airline) NNE Carrizo Tank	31.5516686	-111.561601
Pima18	MK944711/-/-/MK945060/ MK945278/MK945488	bogerti	variegatus	IB3	Arizona, Pima Co.: Baboquivari Mts., Thomas Canyon	31.75065	-111.57682
Pima19	MK944715/-/MK944913/ MK945063/ MK945281/ MK945491	variegatus	variegatus	IB1	Arizona, Pima Co.: South end of Batamote Mts., well in Burro Gap	32.4043	-112.68882
Pima20	MK944716/-/-/-/-/-	variegatus	variegatus	IB1	Arizona, Pima Co.: South end of Batamote Mts., well in Burro Gap	32.4043	-112.68882
Pima21	MK944713/-/-/MK945062/ MK945280/MK945490	variegatus	variegatus	IB1	Arizona, Pima Co.: 3.0 mi (airline) SW Coffeepot Mtn.	32.44245	-112.64362
Pima22	MK944714/-/-/-/-/-	variegatus	variegatus	IB3	Arizona, Pima Co.: 3.0 mi (airline) SW Coffeepot Mtn.	32.44245	-112.64362
Pima23 MVZ245870	MK944674/-/MK944908/ MK945039/ MK945257/ MK945467	bogerti	variegatus	IB3	Arizona, Pima Co.: Greaterville Rd., Santa Rita Mts.	31.79974	-110.78101
Pina0l5	MK944555/-/-/-/-/-	bogerti Xvariegatus	variegatus	IB3	Arizona, Pinal Co.: Sunland-Gin Rd, 0.2 mi S of	32.71609	-111.67158
Pinal01	MK944829/-/-/MK945137/ MK945355/MK945565	variegatus	variegatus	IB3	Arizona, Pinal Co.: near Tabletop Mt. trailhead	32.71385	-112.15688
Pinal02	MK944830/-/-/MK945138/ MK945356/MK945566	variegatus	variegatus	IB3	Arizona, Pinal Co.: near Tabletop Mt. trailhead	32.71602	-112.15843
Pinal03	MK944751/-/-/MK945084/ MK945302/MK945512	bogerti Xvariegatus	variegatus	IB3	Arizona, Pinal Co.: Sunland Gin Road	32.65603	-111.67203
Pinal04	MK944752/-/-/-/-/-	bogerti Xvariegatus	variegatus	IB3	Arizona, Pinal Co.: Sunland Gin Road	32.57069	-111.67278
Pinal06	MK944723/MK944864/-/ MK945069/ MK945287/ MK945497	bogerti	variegatus	IB3	Arizona, Pinal Co.: 1.5 mi (by Houser Rd) N Brady Pump Rd.	32.7775409	-111.4514372

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Pinal07	MK944553/-/-/-/-/-	bogerti	variegatus	IB3	Arizona, Pinal Co.: 4.1 mi W of Brady Pump Rd on Houser Rd	32.7779	-111.48511
Pinal08	MK944697/-/-/-/-/-	bogerti	variegatus	IB3	Arizona, Pinal Co.: 7.2 mi (by rd to Kelvin) ESE Florence	32.99467	-111.01883
Pinal09	MK944698/-/-/MK945050/ MK945268/MK945478	bogerti	variegatus	IB3	Arizona, Pinal Co.: 25.6 mi (by rd to Kelvin) ESE Florence	32.9895	-111.11483
Pinal10	MK944708/-/-/-/-/-	bogerti	variegatus	IB3	Arizona, Pinal Co.: Locality: 5.2 mi (by AZ 79) SE Cactus Forest	32.89905	-111.28042
Pinal11	MK944709/-/-/-/-/-	bogerti	variegatus	IB3	Arizona, Pinal Co.: Park Link Drive at I-10	32.5923	-111.33617
Pinal12	MK944720/-/-/-/-/-	bogerti	variegatus	IB3	Arizona, Pinal Co.: Picacho Hwy, 1.4 mi N Harmon Rd.	32.69672	-111.49835
Pinal13	MK944554/-/-/-/-/-	bogerti	variegatus	IB3	Arizona, Pinal Co.: ~0.2 mi S on Picacho Hwy	32.70579	-111.49876
Riverside01	MK944824/MK944884/-/ MK945133/ MK945351/ MK945561	abbotti	variegatus	IB5bi	California, Riverside Co.: Santa Margarita	33.4579	-117.17077
Riverside02	MK944822/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: Skinner Reservoir	33.59976	-117.02641
Riverside03	MK944823/-/MK944937/ MK945132/ MK945350/ MK945560	abbotti	variegatus	IB5bi	California, Riverside Co.: Skinner Reservoir	33.59976	-117.02641
Riverside04	MK944681/-/-/MK945043/ MK945261/MK945471	abbotti	variegatus	IB5bi	California, Riverside Co.: Diamond Valley Lake	33.70586	-117.00887
Riverside05	MK944682/-/-/MK945044/ MK945262/MK945472	abbotti	variegatus	IB5bi	California, Riverside Co.: Diamond Valley Lake	33.70586	-117.00887
Riverside06	MK944683/-/-/MK945045/ MK945263/MK945473	abbotti	variegatus	IB5bi	California, Riverside Co.: Diamond Valley Lake	33.70586	-117.00887
Riverside07	MK944684/-/-/MK945046/ MK945264/MK945474	abbotti	variegatus	IB5bi	California, Riverside Co.: Diamond Valley Lake	33.70679	-117.00953
Riverside08	MK944678/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: Diamond Valley Lake	33.70547	-117.00808
Riverside09	MK944679/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: Diamond Valley Lake	33.70653	-117.00835

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Riverside10	MK944680/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: Diamond Valley Lake	33.69774	-117.02082
Riverside11	MK944657/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: NW Perris	33.80981	-117.25637
Riverside12	MK944658/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: NW Perris	33.80981	-117.25637
Riverside13	MK944659/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: NW Perris	33.80733	-117.25724
Riverside14	MK944660/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: NW Perris	33.80496	-117.25403
Riverside15	MK944685/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: Lake Perris	33.86303	-117.20209
Riverside16	MK944686/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: Lake Perris	33.88665	-117.1376
Riverside17	MK944687/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: Lake Perris	33.8686	-117.19024
Riverside18	MK944688/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: Lake Perris	33.8686	-117.19024
Riverside19	MK944689/-/-/-/-/-	abbotti	variegatus	IB5bi	California, Riverside Co.: Lake Perris	33.86303	-117.20209
Riverside20 MVZ232696	MK944672/-/-/MK945038/ MK945256/MK945466	abbotti Xvariegatus	variegatus	IB5	California, Riverside Co.: .2 miles north of Dunkel Spring	33.8992	-116.74467
Riverside21	MK944652/-/-/MK945028/ MK945246/MK945456	variegatus	variegatus	IB5	California, Riverside Co.: vicinity of Whitewater	33.96211	-116.66023
Riverside22	MK944653/-/-/-/-/-	variegatus	variegatus	IA	California, Riverside Co.: vic Whitewater	33.96211	-116.66023
Riverside23	MK944654/-/-/MK945029/ MK945247/MK945457	variegatus	variegatus	IA	California, Riverside Co.: vicinity of Whitewater	33.95169	-116.67109
Riverside24	MK944655/-/-/-/-/-	variegatus	variegatus	IA	California, Riverside Co.: vic Whitewater	33.95169	-116.67109
Riverside25	MK944656/-/-/-/-/-	variegatus	variegatus	IA	California, Riverside Co.: vic Whitewater	33.95399	-116.65786
Riverside26	MK944634/-/-/-/-/-	variegatus	variegatus	IA	California, Riverside Co.: Joshua Tree NP	33.84773	-115.77888
Riverside27	MK944635/-/-/MK945020/ MK945238/MK945448	variegatus	variegatus	IB5	California, Riverside Co.: Joshua Tree NP	33.92751	-115.93664

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Riverside28	MK944636/-/-/MK945021/ MK945239/MK945449	variegatus	variegatus	IB5	California, Riverside Co.: Joshua Tree NP	33.8424	-115.75172
Riverside29	MK944637/-/-/MK945022/ MK945240/MK945450	variegatus	variegatus	IA	California, Riverside Co.: Joshua Tree NP	33.92751	-115.93664
Riverside30	MK944638/-/-/-/-/-	variegatus	variegatus	IB5	California, Riverside Co.: Joshua Tree NP	33.92751	-115.93664
Riverside31	MK944639/-/-/MK945023/ MK945241/MK945451	variegatus	variegatus	IA	California, Riverside Co.: Joshua Tree NP, 18 mi N Cottonwood	33.92516	-115.89838
Riverside32	MK944640/-/-/-/-/-	variegatus	variegatus	IB5	California, Riverside Co.: Joshua Tree NP	33.92751	-115.93664
Riverside33	MK944641/-/-/-/-/-	variegatus	variegatus	IB5	California, Riverside Co.: Joshua Tree NP	33.92751	-115.93664
Riverside34	MK944642/-/-/-/-/-	variegatus	variegatus	IB5	California, Riverside Co.: Joshua Tree NP	33.92751	-115.93664
Riverside35	MK944632/-/-/MK945019/ MK945237/MK945447	variegatus	variegatus	IB5	California, Riverside Co.: Joshua Tree NP	33.8424	-115.75172
Riverside36	MK944633/-/-/-/-/-	variegatus	variegatus	IB5	California, Riverside Co.: Joshua Tree NP	33.85366	-115.78569
Riverside37	MK944728/-/-/-/-/-	variegatus	variegatus	IA	California, Riverside Co.: Joshua Tree NP	33.85366	-115.78569
Riverside38	MK944599/-/MK944898/ MK944993/MK945211/ MK945421	variegatus	variegatus	IB5	California, Riverside Co.: Chuckwalla Valley	33.618	-115.13356
Riverside39	MK944646/-/-/MK945025/ MK945243/MK945453	variegatus	variegatus	IA	California, Riverside Co.: ~21 mi. NW of Blythe via Midland Rd	33.8628	-114.7892
SanBernardino01	MK944536/-/-/MK944957/ MK945175/MK945385	variegatus	variegatus	IA	California, San Bernardino Co.: Burns	34.14783	-116.45299
SanBernardino02	MK944537/-/-/-/-/-	variegatus	variegatus	IB5	California, San Bernardino Co.: Burns	34.14413	-116.45198
SanBernardino03	MK944538/-/-/MK944958/ MK945176/MK945386	variegatus	variegatus	IB5	California, San Bernardino Co.: Burns	34.14783	-116.45299
SanBernardino04	MK944539/-/-/-/-/-	variegatus	variegatus	IB5	California, San Bernardino Co.: Burns	34.14783	-116.45299
SanBernardino05	MK944528/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: NW Twentynine Palms	34.20709	-116.15103

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
SanBernardino06	MK944529/-/-/MK944953/ MK945171/MK945381	variegatus	variegatus	IA	California, San Bernardino Co.: NW Twentynine Palms	34.22413	-116.14304
SanBernardino07	MK944530/-/-/MK944954/ MK945172/MK945382	variegatus	variegatus	IA	California, San Bernardino Co.: NW Twentynine Palms	34.20351	-116.14042
SanBernardino08	MK944531/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: NW Twentynine Palms	34.22413	-116.14304
SanBernardino09	MK944532/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: NW Twentynine Palms	34.22413	-116.14304
SanBernardino10	MK944533/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: NW Twentynine Palms	34.22413	-116.14304
SanBernardino11	MK944647/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: 29 Palms Marine Corps Base	34.30291	-116.29786
SanBernardino12	MK944648/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: 29 Palms Marine Corps Base	34.32337	-116.28759
SanBernardino13	MK944649/-/-/MK945026/ MK945244/MK945454	variegatus	variegatus	IA	California, San Bernardino Co.: 29 Palms Marine Corps Base	34.30333	-116.30005
SanBernardino14	MK944650/-/-/MK945027/ MK945245/MK945455	variegatus	variegatus	IA	California, San Bernardino Co.: 29 Palms Marine Corps Base	34.32337	-116.28759
SanBernardino15	MK944651/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: 29 Palms Marine Corps Base	34.30333	-116.30005
SanBernardino16	MK944839/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: Fortynine Palms Oasis	34.1064	-116.10355
SanBernardino17 ROM14676	MK944729/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: Ludlow, Mojave desert 18 mi east on route 66 (just east of Hector off-ramp, vicinity of Pisgah Crater)	34.7859	-116.4427

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
SanBernardino18 ROM14682	MK944730/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: Ludlow, Mojave desert 18 mi east on route 66 (just east of Hector off-ramp, vicinity of Pisgah Crater)	34.7859	-116.4427
SanBernardino19 ROM14700	MK944731/MK944865/-/MK945072/ MK945290/MK945500	variegatus	variegatus	IA	California, San Bernardino Co.: Ludlow, Mojave desert 21.5 mi east on route 66 (east of Hector off-ramp, west edge of Pisgah Crater)	34.77704	-116.3706
SanBernardino20 ROM14701	MK944732/-/-/MK945073/MK945291/MK945501	variegatus	variegatus	IA	California, San Bernardino Co.: Ludlow, Mojave desert 21.5 mi east on route 66 (east of Hector off-ramp, west edge of Pisgah Crater)	34.77704	-116.3706
SanBernardino21 ROM14713	MK944733/MK944866/MK944915/ MK945074/MK945292/MK945502	variegatus	variegatus	IA	California, San Bernardino Co.: Ludlow, Mojave desert 18 mi east on route 66 (just east of Hector off-ramp, vicinity of Pisgah Crater)	34.7859	-116.4427
SanBernardino22	MK944643/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: Hwy 66 east of Barstow	34.7583	-116.3439
SanBernardino23	MK944645/-/-/MK945024/MK945242/MK945452	variegatus	variegatus	IA	California, San Bernardino Co.: Old Trails Hwy Route 66	34.80278	-116.43861
SanBernardino24	MK944603/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: Pisgah Crater	34.81722	-116.34021
SanBernardino25	MK944565/-/MK944889/MK944971/MK945189/MK945399	variegatus	variegatus	IA	California, San Bernardino Co.: Goffs	34.88241	-115.10309
SanBernardino26	MK944616/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: Kelbaker	34.85688	-115.63492

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
SanBernardino27	MK944617/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: Kelbaker	34.87535	-115.64404
SanBernardino28	MK944618/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: Kelbaker	34.88925	-115.65008
SanBernardino29	MK944619/-/-/MK945012/MK945230/MK945440	variegatus	variegatus	IA	California, San Bernardino Co.: Kelbaker	34.95107	-115.64279
SanBernardino30	MK944620/-/-/MK945013/MK945231/MK945441	variegatus	variegatus	IA	California, San Bernardino Co.: Kelbaker	35.20874	-115.87452
SanBernardino31	MK944559/-/-/-/-/-	variegatus	variegatus	IA	California, San Bernardino Co.: 4.1 S of Baker on Kelbaker Rd	35.25652	-116.00172
SanBernardino32	MK944558/-/MK944888/MK944965/MK945183/MK945393	variegatus	variegatus	V	California, San Bernardino Co.: Hwy 127 S of Little Dumont Dunes	35.67642	-116.29964
SanBernardino33	MK944578/-/MK944891/MK944977/MK945195/MK945405	variegatus	variegatus	IA	California, San Bernardino Co.: Kingston Road	35.45773	-115.6861
SanBernardino34	MK944579/-/-/MK944978/MK945196/MK945406	variegatus	variegatus	IA	California, San Bernardino Co.: Kingston Road	35.50652	-115.70361
SanBernardino35	MK944580/-/-/MK944979/MK945197/MK945407	variegatus	variegatus	IA	California, San Bernardino Co.: Kingston Road	35.47181	-115.69786
SanBernardino36	MK944581/-/MK944892/MK944980/MK945198/MK945408	variegatus	variegatus	IVB	California, San Bernardino Co.: Kingston Road	35.46494	-115.68738
SanBernardino37	MK944621/-/-/-/-/-	variegatus	variegatus	IVB	California, San Bernardino Co.: Ivanpah Valley Road	35.39154	-115.35939
SanBernardino38	MK944622/-/-/MK945014/MK945232/MK945442	variegatus	variegatus	IVB	California, San Bernardino Co.: Ivanpah Valley Road	35.3876	-115.35575
SanBernardino39	MK944623/-/-/MK945015/MK945233/MK945443	variegatus	variegatus	IVB	California, San Bernardino Co.: Ivanpah Valley Road	35.39826	-115.36497
SanDiego01	MK944540/-/-/MK944959/MK945177/MK945387	abbotti	variegatus	IB5bi	California, San Diego Co.: Marine Corps Base Camp Pendleton	33.469	-117.47946
SanDiego02	MK944541/-/-/MK944960/MK945178/MK945388	abbotti	variegatus	IB5bi	California, San Diego Co.: Marine Corps Base Camp Pendleton	33.46885	-117.48012

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
SanDiego20	MK944725/-/-/-/-/-	variegatus	variegatus	IB5	California, San Diego Co.: Anza Borrego 1.4 mi. W. County Line	33.14	-116.103
SanDiego21	MK944726/-/-/-/-/-	variegatus	variegatus	IB5	California, San Diego Co.: Anza Borrego 9.8 mi. W. County Line	33.157	-116.245
SanDiego22	MK944525/-/-/-/-/-	variegatus	variegatus	IB5	California, San Diego Co.: S2 NW of Ocotillo	32.8002	-116.11603
SanDiego23	MK944834/-/-/MK945141/ MK945359/MK945569	variegatus	variegatus	IB5	California, San Diego Co.: Borrego Springs	33.2574	-116.319
SanDiego24	MK944560/-/-/MK944966/ MK945184/MK945394	variegatus	variegatus	IB5	California, San Diego Co.: Palo Verde Wash	33.16171	-116.08515
SantaCruz1	MK944693/-/-/MK945048/ MK945266/MK945476	bogerti	variegatus	IB3	Arizona, Santa Cruz Co.: ~ 3.5 mi (airline) WNW Elgin	31.659017	-110.57723
Sonora12	MK944818/-/MK944935/ MK945128/ MK945346/ MK945556	sonoriensis Xvariegatus	variegatus	IB4	Sonora: El Desemboque	30.57113	-113.00001
Washington1	MK944601/-/-/MK944997/ MK945215/MK945425	utahensis	variegatus	IVA	Utah, Washington Co.: vic. Ivins	37.207	-113.701
Washington2	MK944602/-/-/MK944998/ MK945216/MK945426	utahensis	variegatus	IVA	Utah, Washington Co.: vic. Ivins	37.207	-113.701
Washington3	MK944690/-/MK944900/ MK944999/ MK945217/ MK945427	utahensis	variegatus	IVA	Utah, Washington Co.: Quail Creek Reservoir	37.1759	-113.3971
Washington4	MK944691/MK944860/-/ MK945000/ MK945218/ MK945428	utahensis	variegatus	IVA	Utah, Washington Co.: Quail Creek Reservoir	37.1759	-113.3971
Yavapai1	MK944704/-/MK944910/ MK945055/ MK945273/ MK945483	variegatus	variegatus	IB1	Arizona, Yavapai Co.: Vicinity of Yarnell	34.209	-112.76683
Yuma1	MK944556/-/MK944887/ MK944964/MK945182/ MK945392	variegatus	variegatus	IB5	Arizona, Yuma Co.: Somerton on 24th Road off of Avenue E	32.48027	-114.68659
Yuma2	MK944557/-/-/-/-/-	variegatus	variegatus	IB5	Arizona, Yuma Co.:24th Avenue ~1.0 mi F of Ave F	32.48017	-114.71591
Yuma3	MK944598/-/-/MK944992/ MK945210/MK945420	variegatus	variegatus	IB1	Arizona, Yuma Co.: Aztec	32.82628	-113.44285

Appendix. Continued

Study ID & Museum No.	Genbank (*ND1, Cytb, BACH1, NKTR, PRLR, R35*)	Morph. Subspecies	Molecular Lineage	MtDNA Clade	Locality	Lat.	Long.
Yuma4	MK944570/-/-/MK944973/ MK945191/MK945401	variegatus	variegatus	IB1	Arizona, Yuma Co.: Aztec	32.82632	-113.44269
Yuma5	MK944549/-/-/MK944996/ MK945214/MK945424	variegatus	variegatus	IB1	Arizona, Yuma Co.: Spot Road	32.8374	-113.352

Abbreviations: TNHC, Texas Natural History Collection; MVZ, Museum of Vertebrate Zoology, UC Berkeley; ROM, Royal Ontario Museum.