Molecular Ecology (2006) **15**, 2201–2222 doi: 10.1111/j.1365-294X.2006.02930.x

Comparative phylogeography of woodland reptiles in California: repeated patterns of cladogenesis and population expansion

CHRIS R. FELDMAN* and GREG S. SPICER†
*Department of Biology, Utah State University, Logan, Utah 84322-5305, USA,
†Department of Biology, San Francisco State University, 1600 Holloway Ave., San Francisco, California 94132, USA

Abstract

The ultimate goal of comparative phylogeographical analyses is to infer processes of diversification from contemporary geographical patterns of genetic diversity. When such studies are employed across diverse groups in an array of communities, it may be difficult to discover common evolutionary and ecological processes associated with diversification. In order to identify taxa that have responded in a similar fashion to historical events, we conducted comparative phylogeographical analyses on a phylogenetically and ecologically limited set of taxa. Here, we focus on a group of squamate reptiles (snakes and lizards) that share similar ecological requirements and generally occupy the same communities in the western USA. At a gross level, deep genetic division in *Contia tenuis*, *Diadophis punctatus*, *Elgaria multicarinata*, the *Charina bottae* complex, and *Lampropeltis zonata* are often concordant in the Transverse Ranges, the Monterey Bay and Sacramento-San Joaquin Delta region, and the southern Sierra Nevada in California. Molecular clock estimates suggest that major phyletic breaks within many of these taxa roughly coincide temporally, and may correspond to important geological events. Furthermore, significant congruence between the phylogeographies of *E. multicarinata* and *L. zonata* suggests that the succession of vicariance and dispersal events in these species progressed in concert. Such congruence suggests that *E. multicarinata* and *L. zonata* have occupied the same communities through time. However, across our entire multi-taxon data set, the sequence of branching events rarely match between sympatric taxa, indicating the importance of subtle differences in life history features as well as random processes in creating unique genetic patterns. Lastly, coalescent and noncoalescent estimates of population expansion suggest that populations in the more southerly distributed clades of *C. tenuis*, *D. punctatus*, *E. multicarinata*, and *L. zonata* have been stable, while populations in more northerly clades appear to have recently expanded. This concerted demographic response is consistent with palaeontological data and previous phylogeographical work that suggests that woodland habitat has become more restricted in southern California, but more widespread in the North during Holocene warming. Future phylogeographical work focusing on allied and ecologically associated taxa may add insight into the ecological and evolutionary processes that yield current patterns of genetic diversity.

Keywords: California, *Charina*, Comparative phylogeography, *Contia*, demographic history, *Diadophis*, *Elgaria*, *Lampropeltis*, tree-mapping

Received 16 September 2005; revision accepted 6 February 2006

Introduction

The geographical distribution of biodiversity is determined by historical processes of vicariance and dispersal as well as ongoing ecological and demographic processes (Brown & Lomolino 1998). Traditional phylogeographical analyses reconstruct ancestor–descendant relationships of populations yielding the relative timing of important historical vicariant events (Avise *et al*. 1987; Avise 1989). Much has been added to such studies through recent advances in our ability to analyse historical demographic patterns allowing inference

Correspondence: Chris R. Feldman, Fax: 435-797-1575; E-mail: elgaria@biology.usu.edu

of past population changes within lineages subsequent to major vicariant events (e.g. Matocq 2002a; Mahoney 2004). When expanded to multiple, codistributed taxa at nearly continental scales, these phylogeographical approaches can provide insight into major historical occurrences that had an overriding effect on numerous taxa (e.g. Hewitt 2000; Wares & Cunningham 2001; Zink 2002; Lessa *et al*. 2003). While such broad taxonomic and geographical comparative studies identify gross patterns of genetic discontinuities due to overriding events such as 'isolation' or 'recolonization', they may not always provide a great deal of insight into the actual evolutionary processes associated with diversification. Diverse species may share coarse-scale patterns of subdivision due to particular barriers, yet because of differences in dispersal capabilities, generation time, breeding structure, effective population size and ecological constraints, it is likely that such taxa arrived at similar patterns of geographical subdivision through very different evolutionary paths. Because evolutionary biologists are ultimately concerned with the processes underlying patterns of diversification, we suggest an alternative multi-taxon approach. By focusing comparative phylogeographical analyses on relatively closely related taxa with largely similar ecological requirements, we may more easily identify taxa that underwent similar evolutionary dynamics in response to overriding historical events (e.g. Riddle *et al*. 2000; Sullivan *et al*. 2000). Furthermore, additional analyses that test phyletic congruence between codistributed forms and examine demographic history within lineages should yield a more comprehensive view of common history (Lapointe & Rissler 2005).

An ideal setting in which to study patterns and processes of diversification is the taxonomically rich and geologically complex region along the coastal margin of the western North America. California, in particular, is a biodiversity hot spot (Myers *et al*. 2000) marked by a complex landscape and dynamic geological history. A unique feature of California is the Great Central Valley, a large expanse of prairie and marsh (now agricultural plots) entirely enclosed by mountains: the Klamath Mountains and Cascade Range to the north, Sierra Nevada Mountains to the east, Transverse Ranges to the south, and Coast Ranges to the west (Fig. 1). Because valley habitat is unsuitable for woodland and forest fauna, a number of species display a ring-like distribution, restricted to the surrounding hills and mountains. Recently, a review of phylogeographical studies in California suggested that historical vicariant events account for a number of deep genetic subdivisions across phyla that occupy a range of habitats (Calsbeek *et al*. 2003). While this study summarized gross patterns of genetic discontinuities across phylogenetically and ecologically disparate groups, it did not address finer levels of congruent branching patterns nor regional demographic history. Our aim was to create a data set that

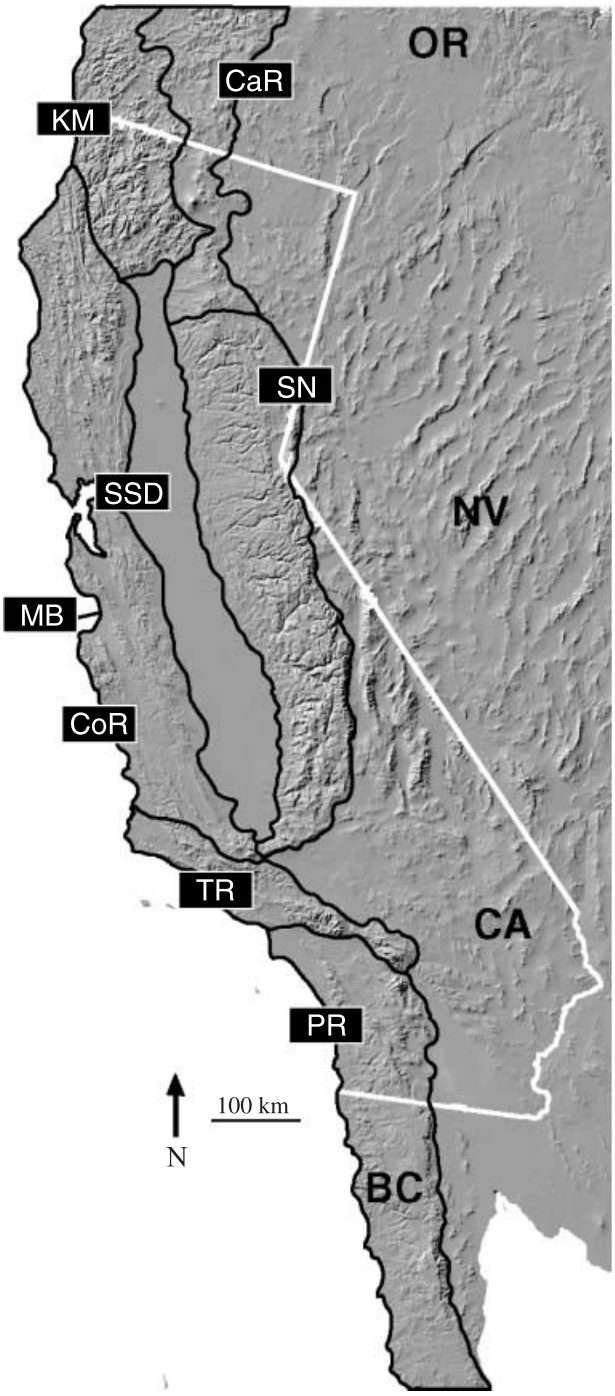

Fig. 1 Map of a portion of western North America featuring southern Oregon (OR), California (CA), Nevada (NV), and northern Baja California (BC). Important physiographic features (after Schoenherr 1992) mentioned in text: CaR, Cascade Range; KM, Klamath Mountains; SN, Sierra Nevada Mountains; CoR, Coast Ranges; TR, Transverse Ranges; PR, Peninsular Ranges; SSD, Sacramento-San Joaquin Delta; MB, Monterey Bay.

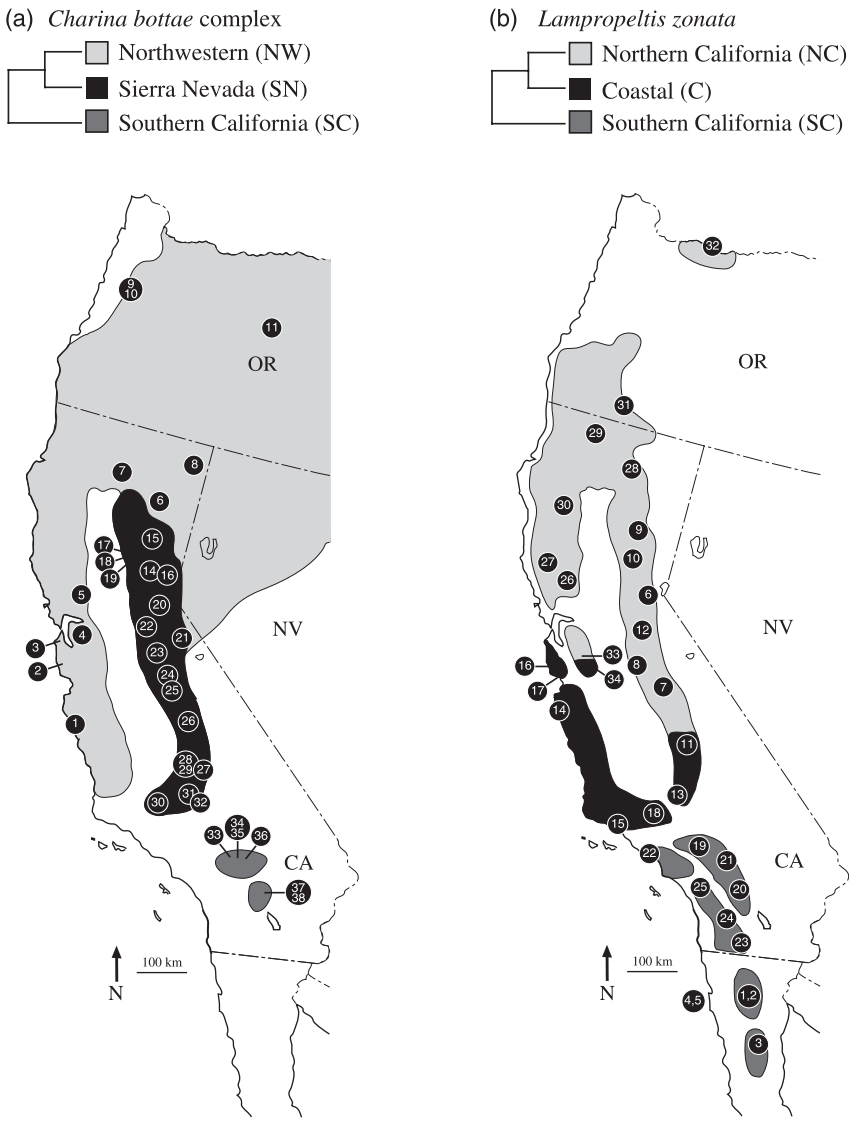

Fig. 2 Simplified phylogeographies and clade distributions of the *Charina bottae* complex (Rodriguez-Robles *et al*. 2001) and *Lampropeltis zonata* (Rodriguez-Robles *et al*. 1999). Sample numbers on map correspond to localities in Appendix. (a) Phylogeography and geographical range the *C. bottae* complex in California, Oregon, and Nevada (after Rodriguez-Robles *et al*. 2001; Stebbins 2003), with approximate distribution of major mtDNA clades. (b) Phylogeography and geographical range of *L. zonata* in California, Oregon, and Baja California (after Rodriguez-Robles *et al*. 1999; Stebbins 2003), with approximate distribution of major mtDNA clades.

would identify, in greater detail, taxa that have responded to major historical events in a similar fashion. In order to identify such taxa, we conducted comparative phylogeographical analyses of a group of relatively closely related taxa that largely share ecological requirements and occupy similar trophic levels. We focused on a group of squamate reptiles that occupy the same communities (chaparral, oak woodland, and mixed pine and oak woodland) and share similar geographical distributions over much of Washington, Oregon, California and Baja California. We collected mitochondrial DNA (mtDNA) sequence data from populations of the sharp-tailed snake (*Contia tenuis*), the ringneck snake (*Diadophis punctatus*), and the southern alligator lizard (*Elgaria multicarinata*). We augmented our three data sets with orthologous sequence data from two previously studied reptile groups, the rubber boas (*Charina bottae* and *Charina umbratica*, herein the *C. bottae* complex; Rodriguez-Robles *et al*. 2001) and the California mountain kingsnake (*Lampropeltis zonata*; Rodriguez-Robles *et al*. 1999) (Fig. 2). However, we did not include like data from the *Eumeces skiltonianus* complex. Populations of the *Eu. skiltonianus* complex that occupy woodland habitats actually belong to several independent groups related to arid adapted lineages, rendering our focal communities paraphyletic (Richmond & Reeder 2002). With this taxonomically and ecologically restricted approach, our goal was to identify, in detail, taxa that possess similar evolutionary responses to major historical events. To achieve this goal, we conducted separate tree-based analyses following a three-tiered approach. First, we explored spatial and temporal links between the major genetic divergences shared across the codistributed reptiles. Second, we compared phylogeographical structure across taxa for evidence of codivergence. Third, we tested for signatures

of population expansions or stability within regional clades. Our spatial and temporal hierarchical approach spans deep phylogenetic structure to recent demographic trends among ecologically and demographically similar taxa. This approach should provide unique insight into the degree of concordant biotic responses to historical events.

Materials and methods

Population sampling

We collected mtDNA sequence data from 29 *Contia tenuis* (25 localities), 39 *Diadophis punctatus* (39 localities) and 45 *Elgaria multicarinata* (42 localities) (Figs 3, 4, and 5; Appendix). We sampled all six West Coast subspecies of *D. punctatus* as well as forms from Arizona and Florida. We also sampled four of the five subspecies of *E. multicarinata*, and included multiple representatives of most other western *Elgaria* species. We deposited specimens collected for this study as vouchers in institutional collections (Appendix). Note that although we sampled only a portion of the total range of *D. punctatus*, the focal region examined here is composed of a geographically allopatric and monophyletic subset of the total diversity in this taxon (F. Fontanella, C. Feldman, F. Burbrink unpublished data).

We also included sequence data from an orthologous mitochondrial region from two previously studied groups, the *Charina bottae* complex and *Lampropeltis zonata*. The 38 *Charina* (35 localities) are from Rodriguez-Robles *et al*. (2001) and the 34 *Lampropeltis* (32 localities) from Rodriguez-Robles *et al*. (1999) (Fig. 2; Appendix). Most of the *C. tenuis* data are from Feldman & Spicer (2002), but we added a number of key geographical samples.

Laboratory protocols

We isolated genomic DNA from liver tissue, scales, shed skin and tail tips, by standard proteinase K digestion and phenol–chloroform purification (Maniatis *et al*. 1982). We amplified 900 bp of mtDNA encoding a section of ND4 and flanking $tRNA^{his}$, $tRNA^{ser}$, and $tRNA^{leu}$ via polymerase chain reaction (PCR) (Saiki *et al*. 1988) using primers ND4 (5′-CACCTATGACTACCAAAAGCTCATGTAGAAGC-3′) and Leu (5′-ACCACGTTTAGGTTCATTTTCATTAC-3′) (Arevalo *et al*. 1994). We used the following PCR conditions for 50 μL amplification reactions: 35 cycles of 1 min 94 °C, 1 min 52 °C, and 2 min 72 °C. We purified PCR products using the Wizard Prep Mini Column Purification Kit (Promega, Inc.) and used purified template in 10 μL dideoxy chain-termination reactions (Sanger *et al*. 1977) using ABI Big Dye chemistry (Applied Biosystems, Inc.) and the primers listed above. Following an isopropanol/ethanol precipitation, we ran cycle-sequenced products on a 4.8% Page Plus (Ameresco) acrylamide gel using an ABI 377 automated sequencer (Applied Biosystems, Inc.). We sequenced all samples in both directions.

Sequence analyses

We aligned DNA sequences with the program SEQUENCHER 4.1 (Gene Codes Corp.), and translated protein coding nucleotide sequences into amino acid sequences using MACCLADE 4.0 (Maddison & Maddison 2000). We identified tRNA genes by manually reconstructing their secondary structures using the criteria of Kumazawa & Nishida (1993). We deposited all mtDNA sequences in GenBank (Appendix).

Phylogenetic analyses

We used maximum parsimony (MP; Farris 1983) and maximum likelihood-based (ML; Felsenstein 1981) Bayesian inference (BI; Larget & Simon 1999) to infer evolutionary relationships among haplotypes. We conducted MP analyses in PAUP* 4.0b10 (Swofford 2002) and BI analyses with MRBAYES 3.0b4 (Huelsenbeck & Ronquist 2001). We rooted characters using the outgroup method (Maddison *et al*. 1984). While *Diadophis* and *Contia* may be close relatives (Pinou *et al*. 2004), relationships among dipsadoid snakes remain uncertain (Cadle 1984; Zaher 1999; Vidal *et al*. 2000; Pinou *et al*. 2004). Thus, we used both *Heterodon platirhinos* (eastern hognose snake) and *D. punctatus* to root *C. tenuis* sequences, and *H. platirhinos* and *C. tenuis* to root *D. punctatus* sequences. We treated all *Elgaria* species as ingroup taxa except *Elgaria coerulea*. Previous morphological data (Good 1988a), biochemical data (Good 1988b; Macey *et al*. 1999), and molecular genetic data (Macey *et al*. 1999) indicate that *E. coerulea* is sister to a clade containing the remaining *Elgaria* species.

We executed MP analyses with a heuristic search algorithm consisting of 1000 replicates of random stepwise-additions of taxa using tree-bisection–reconnection (TBR) branch swapping. We treated characters with equal weight and coded gaps in the tRNAs as fifth character states. To evaluate nodal support, we used the bootstrap resampling method (bootstrap percentage hereafter BP; Felsenstein 1985) employing 1000 full heuristic, pseudoreplicate searches in PAUP*. Additionally, we estimated branch support (decay index hereafter DI; Bremer 1994) for all nodes using the program TREEROT 2c (Sorenson 1999). Here, we consider nodes to be well supported if they were found in ≥ 70% bootstrap replicates (Hillis & Bull 1993).

We determined the most appropriate model of DNA substitution for reconstructing haplotype relationships under BI via hierarchical likelihood ratio tests (hLRT; Felsenstein 1993; Goldman 1993; Yang 1996) in the program MODELTEST 3.06 (Posada & Crandall 1998). The model of nucleotide substitution that best fit the *C. tenuis*, *D. punctatus*, and

E. multicarinata sequence data was the HKY + Γ model (Hasegawa *et al*. 1985; Yang 1994a, 1994b). We executed three separate BI analyses on each data set to be sure that independent analyses converged on similar nodal support values and –ln L scores (Leaché & Reeder 2002). For each BI search, we did not specify model parameters or a topology a priori, and ran BI analyses for 3×10^6 generations using the default temperature (0.2) with four Markov chains per generation, sampling trees every 100 generations. Because the three independent runs for each data set converged on nearly identical nodal support values and –ln L scores, we simply pooled the three separate runs for each data set and computed 50% majority-rule consensus trees after excluding those trees sampled prior to the stable equilibrium, yielding estimates of nodal support given by the frequency of the recovered clade (posterior probability hereafter PP; Rannala & Yang 1996; Huelsenbeck & Ronquist 2001). We consider nodes significantly supported if they were recovered in ≥ 95% of the sampled trees (Huelsenbeck & Ronquist 2001).

Divergence times

We used the mtDNA sequence data to estimate the timing of cladogenic events in well-supported lineages of *C. tenuis*, *D. punctatus*, *E. multicarinata*, the *C. bottae* complex, and *L. zonata*. Such temporal estimates allow us to explore possible links between cladogenesis and known geological events, and uncover instances of parallel diversification in unrelated regional clades.

First, we determined that these mtDNA data are evolving in a clock-like fashion by comparing differences in substitution rates between major intraspecific lineages using a relative-rate test (Sarich & Wilson 1973; Wu & Li 1985). In RRTREE 1.1.9 (Robinson-Rechavi & Huchon 2000) we compared rates between major clades with K2P distances (Kimura 1980), treated sequences as noncoding to include tRNA data, and used sister group sequences rather than outgroup sequences (when possible) to make comparisons to a third group. Note that RRTREE only allows the use of uncorrected or K2P distances. In all but one case, the difference between substitution rates among clades was not significant, thus the sequences met the assumptions of a rate-constant model and were used to make rough estimates of divergence times (Table 2).

Because these species lack adequate fossil records (with the possible exception of the *C. bottae* complex), we cannot make 'internal' rate calibrations (Hillis *et al*. 1996; van Tuinen & Hedges 2001). Therefore, we used an 'external' rate of molecular evolution calibrated from well-characterized geological events for mtDNA. We employed a rate of 1.6% sequence divergence per million years obtained using the Langley-Fitch method (Langley & Fitch 1974) from ML corrected distances of ND4, ND2 and cyt *b* sequences from snakes (Wüster *et al*. 2005; Wüster, personal communication). We calculated separation times by applying this pairwise rate to the average ML corrected distances obtained from PAUP* between major clades.

Despite limiting our analyses to an orthologous gene region in closely allied taxa, the confidence intervals around molecular clock estimates are extensive, leading to inexact estimates that must be interpreted judiciously (Hillis *et al*. 1996; Graur & Martin 2004). Thus, it may be difficult to determine whether a single vicariant event, or multiple events contributed to congruent regional genetic structure across species. To address this issue, we forced our oldest and youngest estimated dates for congruent genetic breaks onto taxa that share the geographical breaks. We then calculated the rates of molecular evolution required to produce such dates given the amount of sequence divergence observed. If the rates of evolution calculated by this method fell outside the known rates of mtDNA evolution for protein coding genes in other squamate reptiles, then we rejected the hypothesis that a single vicariant event similarly influenced cladeogenesis in the codistributed taxa.

Tree-mapping analyses

We evaluated the concordance in phylogeographical structure between *C. tenuis*, *D. punctatus*, *E. multicarinata*, the *C. bottae* complex, and *L. zonata*, by tree-mapping (Page 1994a, b) to determine whether any species show evidence of concerted diversification over the same landscape. Here, the tree-mapping procedure requires geographically overlapping samples and identical numbers of OTUs. Thus, we chose 15 localities (A-O) that possessed overlapping samples (proximate by roughly 50 miles) and provided broad geographical coverage, and pruned the five mtDNA data sets to the samples in those localities (Fig. 6; Appendix). We used the pruned data sets in TREEMAP 1.0b (Page 1994a, b) to determine whether the number of parallel divergence events, termed codivergences (Page 1994b), between *C. tenuis*, *D. punctatus*, *E. multicarinata*, the *C. bottae* complex, and *L. zonata* lineages are nonrandom. In TREEMAP we held the phylogeny of one species constant (*H*; host tree) while optimally fitting the phylogeny of another species (*A*; associate tree) onto tree *H*, noting the number of codivergence events obtained from reconciling tree *A* onto tree *H*. We then randomized tree *A* onto tree *H* 1000 times to generate a null distribution of reconciled codivergence events. The null hypothesis is that the number of codivergences of the optimally fit tree reconciliation is not statistically distinguishable from the distribution of codivergence events obtained from the randomized tree reconciliations expected for taxa that display independent histories. Note, however, that when TREEMAP fits *A* tree onto *H* tree, the method postulates sorting or

dispersal events to reconcile the two phylogenies. Because we have arbitrarily chosen *A* and *H*, we cannot use the hypothesized sorting and dispersal events to draw additional inferences about the exact history of either *A* or *H* taxon.

Demographic analyses

We assessed trends in the demographic histories of *C. tenuis*, *D. punctatus*, *E. multicarinata*, the *C. bottae* complex, and *L. zonata*, by estimating population growth in the major geographical lineages to determine whether regional clades show evidence of concordant patterns of expansion. Tests of demographic history should ideally be applied to groups that possess a single demographic history. Therefore, we restricted our analyses to the specific clades or subclades recognized herein, that by definition share a single history.

First, we used a ML coalescent approach to estimate the exponential population growth rate (g) by sampling genealogies via Metropolis-Hastings Markov chain Monte Carlo (MCMC) method (Kuhner *et al*. 1995, 1998). We estimated g for each group in FLUCTUATE 1.5 (Kuhner *et al*. 1998) using empirical base frequencies and ingroup ti/tv ratios estimated from BI trees. For the *C. bottae* complex and *L. zonata*, we obtained base frequencies and ti/tv ratios from ML topologies recovered by Rodriguez-Robles *et al*. (2001) and Rodriguez-Robles *et al*. (1999) under the HKY + Γ model. We initiated FLUCTUATE analyses with a Watterson (1975) estimate of theta (Θ), a g value of 1, and a random topology, performing 10 short chains, sampling every 50 genealogies for 25 000 steps, and two long chains, sampling every 50 genealogies for 100 000 steps. However, this genealogical method is known to yield estimates of g with an upwards bias (Kuhner *et al*. 1998). Thus, we corrected g values following the conservative approach of Lessa *et al*. (2003) and only considered a g value indicative of population growth when $g > 3$ SD.

As a second measure of demographic expansion, we employed an F_S test (Fu 1997). The F_S test uses a noncoalescent estimate of theta weighted by haplotype frequency (θ_p) to detect an excess of 'young' haplotypes expected in an expanding population (Fu 1997). We calculated both F_S and θ_p values using uncorrected distances and assessed the significance of our F_S scores with 1000 random permutations in ARLEQUIN 2.0 (Schneider *et al*. 2000).

To identify the spatial extent of population expansion and stability, we reported g, F_S and θ_p values for lineages positioned south, central, and north of each other (determined by the centre of a clade's distribution). Note that actual values of g are specific to each taxon, and cannot be compared across species, so we only compared g values within each taxon and trends in g across taxa.

Results

Genetic variation

The sequences from the protein-coding gene ND4 appear functional. In addition, we did not find any tRNA rearrangements and the secondary structures of $tRNA^{his}$ and $tRNA^{ser}$ are consistent with those of other squamate reptiles (Kumazawa & Nishida 1995; Kumazawa *et al*. 1996; Macey & Verma 1997; Macey *et al*. 1997). The final sequenced product was over 850 bp for the *Contia tenuis*, *Diadophis punctatus*, and *Elgaria multicarinata* data sets (Table 1), similar in size to the orthologous loci sequenced by Rodriguez-Robles *et al*. (2001) for the *Charina bottae* complex and Rodriguez-Robles *et al*. (1999) for *Lampropeltis zonata* (Table 1). Given the population level focus of this study, ND4 and the linked tRNAs provided a high proportion of parsimony informative characters across all data sets and sizeable number of haplotypes despite the relatively small geographical scale (Table 1).

Contia tenuis *Phylogeography*

Both MP and BI analyses reveal a deep split between *C. tenuis* populations in California and Oregon into two major clades: a coastal clade and an interior/Sierra Nevada clade (Feldman & Spicer 2002) (Fig. 3). *Contia tenuis* of the coastal clade (BP 100, DI 21, PP 100) occur from the Santa Cruz Mountains to the coastal margins of the northern Coast Range and Klamath mountains (samples 22–29). Sharp-tailed snakes of the widespread interior/Sierra Nevada clade (BP 100, DI 13, PP 95) occur in the Sierra Nevada Mountains, Cascade Range, Klamath Mountains, central Coast Range, and the interior portion of the northern Coast Range (samples 1–21). The interior/Sierra Nevada clade can be further divided into two well-supported subclades: an interior/Sierra Nevada subclade and a southern Sierra Nevada subclade. The interior/Sierra Nevada subclade (BP 93, DI 3, PP 79) consists of populations that occupy the majority of the interior/Sierra Nevada clade range (samples 1–18). Additional structure within the interior/Sierra Nevada subclade is not geographically apportioned. For example, a single haplotype (I/SN5) occurs in disparate regions from the interior Coast Ranges, to the mid-Sierra Nevada, while another population (samples 5, 6) possesses haplotypes in separate groups. In contrast to the wide-ranging interior/Sierra Nevada subclade, the southern Sierra Nevada subclade (BP 100, DI 10, PP 100) appears restricted to the southern end of the Sierra Nevada Mountains (samples 19–21).

Diadophis punctatus *Phylogeography*

The MP and BI methods group the western ringneck snakes (samples 1–39) to the exclusion of *Diadophis punctatus*

Table 1 Summary statistics from the mtDNA data for the three new squamate data sets including results from the MP and BI analyses. Parameter estimates from BI analyses represent mean values from consensus trees based on the nearly 30 000 sampled BI trees

	Contia tenuis	*Diadophis punctatus*	*Elgaria multicarinata*
No. of characters (ND4/tRNA)	860 (696/164)	855 (696/159)	856 (695/158)
No. of parsimony informative sites	113	110	165
No. of ingroup parsimony informative sites	81	55	134
No. of tRNA indels	7	10	1
No. of ingroup samples	29	39	57
No. of unique ingroup haplotypes	17	23	47
MP tree score (L)	313	399	315
CI/RI	0.914/0.956	0.852/0.813	0.721/0.931
No. of MP trees	4	3	72
Model of sequence evolution	HKY + Γ	HKY + Γ	HKY + Γ
Mean BI tree score (– ln L)	2551.610	2900.730	3151.110
Mean ti/tv ratio estimate	3.870	4.464	7.685
Mean ingroup ti/tv ratio estimate[a]	5.995	5.843	6.359
Mean gamma estimate (α)	0.324	0.262	0.085

[a]We estimated ingroup ti/tv ratios from BI consensus phylograms in PAUP* by excluding outgroup sequences. We then used these values for subsequent estimates of *g* in FLUCTUATE.

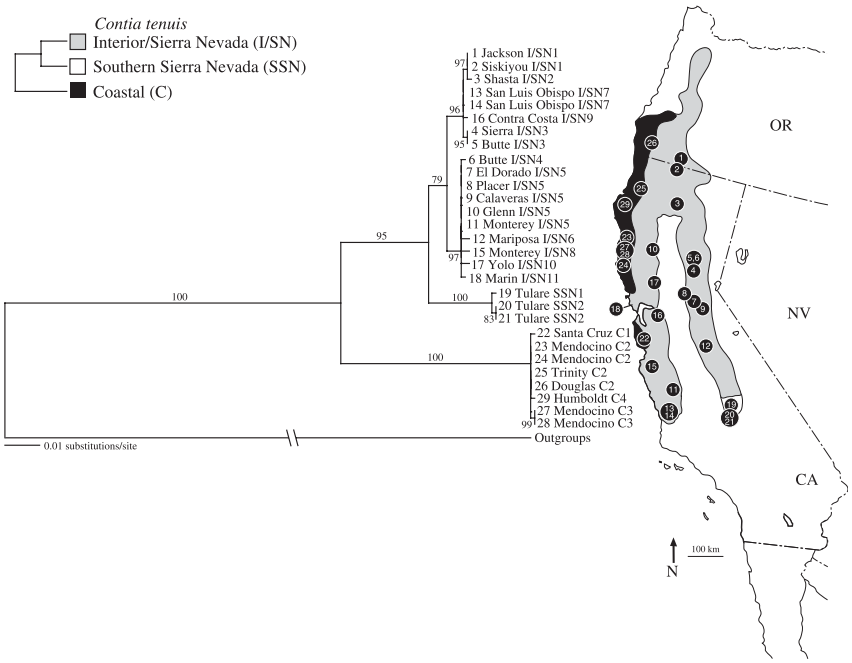

Fig. 3 Phylogenetic relationships of *Contia* mtDNA lineages based on HKY + Γ BI analysis. Sample number, county, and clade-specific haplotype is given for each individual; sample numbers on tree correspond to localities on map and in Appendix. Numbers along node indicate BI posterior probabilities; branch lengths are drawn proportional to BI estimates of genetic divergence. Geographical range of *Contia tenuis* in California and Oregon (after Leonard & Ovaska 1998; Hoyer 2001; Stebbins 2003), with approximate distribution of major mtDNA clades.

punctatus from Florida (sample 40) (Fig. 4). Within this western clade (BP 100, DI 11, PP 100), populations along the West Coast (samples 1–37) form a monophyletic group (BP 92, DI 6, PP 97) sister to a *Diadophis punctatus regalis* clade (BP 100, DI 7, PP 100) from southeastern California and Arizona (samples 38, 39). Finally, both MP and BI trees show a basal divergence between *D. punctatus* populations in California into two major lineages: a northern California clade and a southern California clade. *Diadophis punctatus* of the widespread northern California clade (BP 53, DI 0, PP 51) occur in the Transverse Ranges, Coast Ranges, Cascade Range, Sierra Nevada Mountains and the Klamath Mountains of California and Oregon (samples 1–31). This group possesses virtually no geographical structure. For example, a single haplotype (NC1) is found in 14 separate localities, from northwestern Oregon, to the San Francisco Bay area, to the southern Sierra Nevada. Ringneck snakes of the southern California clade (BP 88, DI 3, PP 100) are restricted in the Transverse and Peninsular Ranges of southern California, from the Los Angeles Basin through San Diego (samples 32–37). The southern California clade also contains nested subclades characterized by strong phylogeographical structure.

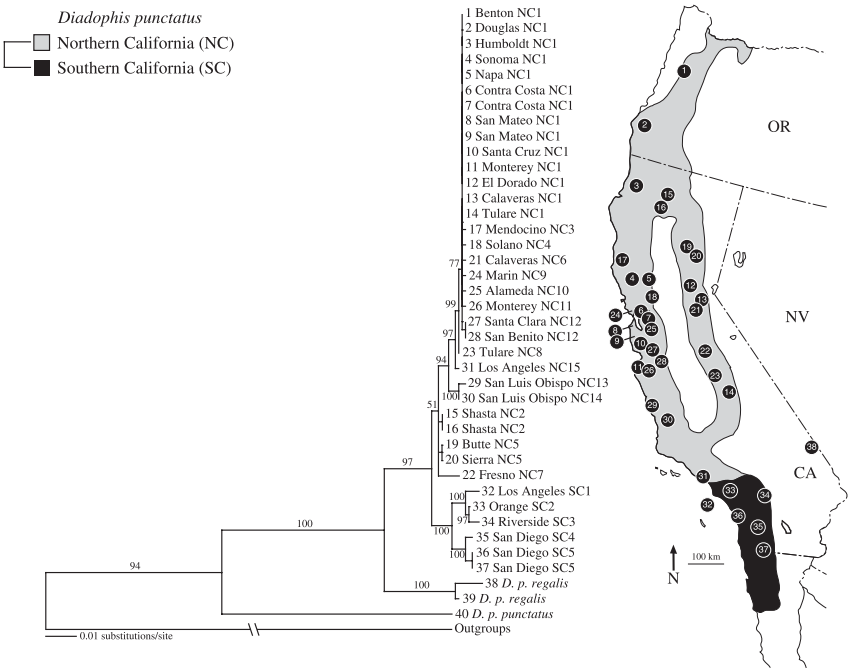

Fig. 4 Phylogenetic relationships of *Diadophis* mtDNA lineages based on HKY + Γ BI analysis. Sample number, county, and clade-specific haplotype is given for each individual; sample numbers on tree correspond to localities on map and in Appendix. Numbers along node indicate BI posterior probabilities; branch lengths are drawn proportional to BI estimates of genetic divergence. Geographical range of *Diadophis punctatus* in California, Oregon, and Baja California (after Blanchard 1942; Stebbins 2003), with approximate distribution of major mtDNA clades.

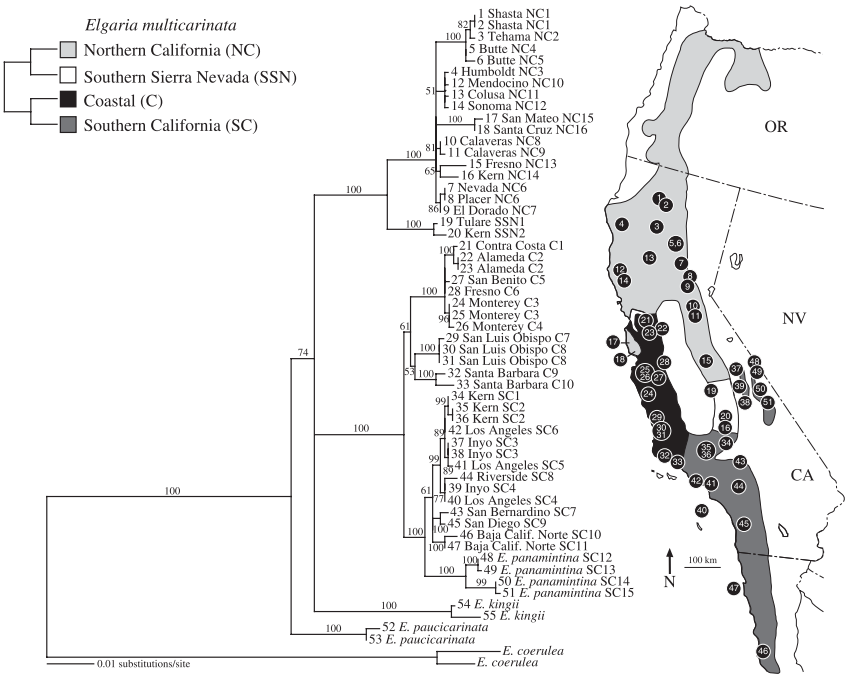

Fig. 5 Phylogenetic relationships of *Elgaria* mtDNA lineages based on HKY + Γ BI analysis. Sample number, county, and clade-specific haplotype is given for each individual; sample numbers on tree correspond to localities on map and in Appendix. Numbers along node indicate BI posterior probabilities; branch lengths are drawn proportional to BI estimates of genetic divergence. Geographical range of *Elgaria multicarinata* and *Elgaria panamintina* in California, Oregon, and Baja California (after Lais 1976; Stebbins 2003), with approximate distribution of major mtDNA clades.

Elgaria multicarinata *Phylogeography*

Both MP and BI phylogenetic methods recover four major ingroup lineages (samples 1–55): an *Elgaria kingii* clade (BP 100, DI 12, PP 100), an *Elgaria paucicarinata* clade (BP 100, DI 13, PP 100), a northern California *E. multicarinata* clade (BP 97, DI 8, PP 100), and a southern California *E. multicarinata* clade (BP 100, DI 10, PP 100) (Fig. 5). However, relationships between these major mtDNA clades remain uncertain. In fact, the split between the northern and southern California *E. multicarinata* clades is of such a magnitude that it is unclear whether these groups are each other's closest relatives. A strict consensus of the equally parsimonious trees provides no resolution for relationships among these four *Elgaria* lineages (BP < 50, DI 0). The Bayesian inferred phylogeny, on the other hand, places *E. kingii* and the two

E. multicarinata clades into a trichotomy, and again assigns *E. paucicarinata* sister to this group with no support (PP 74).

Despite uncertainties in the higher-level relationships of *Elgaria*, both MP and BI analyses recover two deep mtDNA lineages of *E. multicarinata* in California. *Elgaria multicarinata* of the northern California clade are found from the southern tip of the Sierra Nevada, north into the Cascade Range and Klamath mountains and south along the Coast Ranges to the Santa Cruz Mountains (samples 1–20). The northern California clade can be further separated into two well-supported subclades: a northern California subclade and a southern Sierra Nevada subclade. The northern California subclade (BP 97, DI 6, PP 100) is comprised of nearly all other northern California clade populations (samples 1–18) and exhibits additional hierarchical population genetic structure congruent with geography. The southern Sierra Nevada subclade (BP 100, DI 8, PP 100) appears restricted to the Greenhorn Mountains and southwestern foothills of the Sierra Nevada (samples 19, 20). Alligator lizards of the southern California clade occur from the central Coast Ranges, South to middle Baja California and East into portions of the Mojave and Great Basin Deserts (samples 21–51). Two additional groups exist within the southern California clade: a coastal subclade, and a southern California subclade. The coastal subclade (BP 71, DI 1, PP 61) appears limited to the central Coast Ranges and western margin of the Transverse Ranges (samples 21–33). The more extensive southern California subclade (BP 70, DI 1, PP 100) occurs from the Transverse Ranges and Tehachapi Mountains south through the Peninsular Ranges into Baja California (samples 34–36, 40–46) and extends east of the Sierra Nevada to disjunct populations in the Owens Valley (samples 37–39). The southern California subclade also includes *Elgaria panamintina* (BP 100, DI 7, PP 100), endemic to the White, Inyo, and Panamint mountains (samples 48–51). As in the northern California subclade, both the coastal and the southern California subclades contain additional nested groups, most of which display fine-scale regional integrity and receive high statistical support.

Divergence times

Divergence estimates suggest that the major geographical lineages recognized herein diversified from the Miocene/Pliocene to the Pliocene/Pleistocene (Table 2). Cladogenic estimates range from a high of over 5 million years ago (Ma) between the two main *Contia* clades, to under 2 Ma between the two California *Diadophis* clades (Table 2).

Table 2 Divergence estimates between chief geographical mtDNA lineages of *Contia tenuis*, *Diadophis punctatus*, *Elgaria multicarinata*, the *Charina bottae* complex and *Lampropeltis zonata*. Geographical split refers to the general location of a genetic break between major haplotype groups. We assessed differences in ND4 substitution rates (dK) between sister clades via relative-rate test. We estimated divergence times using a pairwise rate of 1.6% sequence divergence per million years (Wüster *et al*. 2005; Wüster, personal communication) with average ML corrected distances. We also calculated low and high rates of molecular evolution by forcing high and low divergence dates onto taxa that share a geographical break. We considered evolutionary rates beyond those seen in mtDNA-encoding regions in squamates (indicated with *) as evidence that a single vicariant event does not explain the shared genetic break

Geographical split Clade or subclade divergence being timed	dK	*P* value	ML distance (mean %)	Cladogenic est. (Ma)	Low rate (%/my)	High rate (%/my)
Transverse Ranges						
D. punctatus northern California & southern California clades	–0.002	0.616	2.38	1.49	0.4*	1.6
E. multicarinata coastal & southern California subclades	0.001	0.775	2.60	1.63	0.5	1.7
C. bottae cmplx northwestern & southern California clades	–0.005	0.636	8.49	5.31	1.6	5.7*
L. zonata northern California & southern California clades	–0.001	0.903	5.35	3.33	1.0	3.6*
Monterey Bay/Sacramento-San Joaquin Delta						
E. multicarinata northern California & southern California clades	0.002	0.758	7.01	4.38	1.6	2.1
L. zonata northern California & coastal subclades	0.007	0.299	5.37	3.36	1.2	1.6
Southern Sierra Nevada						
C. tenuis interior/Sierra Nevada & southern Sierra Nevada subclades	–0.006	0.285	2.91	1.82	1.4	1.6
E. multicarinata northern California & southern Sierra Nevada subclades Cascade Range/Sierra Nevada	0.003	0.569	3.38	2.11	1.6	1.9
C. bottae cmplx northwestern & Sierra Nevada subclades	–0.012	0.061	5.39	3.37	—	—
Interior Coast Ranges						
C. tenuis coastal & interior/Sierra Nevada clades	–0.005	0.653	9.01	5.63	—	—
Mojave and Great Basin Deserts						
D. punctatus West Coast & *D. p. regalis* clades	0.001	0.859	4.85	3.03	—	—
E. multicarinata southern California & *E. panamintina* subclades	–0.013	0.007	2.56	—	—	—

Table 3 Results of tree-mapping analysis. Numbers above diagonal represent the number of codivergences based on optimal tree reconciliations, while numbers below the diagonal are associated *P* values based on a null distribution of randomly reconciled trees. Only *Elgaria multicarinata* and *Lampropeltis zonata* show evidence of a shared history

	C. tenuis	*D. punctatus*	*E. multicarinata*	*C. bottae cmplx*	*L. zonata*
C. tenuis	—	4	3	2	2
D. punctatus	0.283	—	5	3	4
E. multicarinata	0.666	0.230	—	3	7
C. bottae cmplx	0.852	0.599	0.612	—	4
L. zonata	0.892	0.410	0.015	0.103	—

These mtDNA data suggest at least three instances of concerted cladogenesis in areas with congruent genetic breaks: (i) the southern Sierra Nevada; (ii) the Monterey Bay and Sacramento-San Joaquin Delta; (iii) the Transverse Ranges. In the southern Sierra Nevada, subclades of *C. tenuis* and *E. multicarinata* are estimated to have separated roughly 2 Ma from their respective sister groups. In the Monterey Bay and Sacramento-San Joaquin Delta region, we estimated that the two deepest clades of *E. multicarinata* split over 4 Ma, and the northern and coastal clades of *L. zonata* over 3 Ma. However, in the Transverse Ranges, matching temporal diversification is more difficult to demonstrate. While four of the five taxa show grossly concordant phylogenetic breaks in the Transverse Ranges, the divergence estimates vary from 5 Ma in the *C. bottae* complex, to 3 Ma in *L. zonata*, to under 2 Ma in *D. punctatus* and *E. multicarinata*. To determine whether congruent phyletic structure in southern California is the result of a single vicariant event, or multiple events, we forced our oldest and youngest estimated divergence dates onto the four taxa that share this phylogeographical pattern. The low rates of molecular evolution required to produce the oldest date (*C. bottae* complex; 5.31 Ma) do not fall outside the known rates of evolution for encoding mtDNA genes seen in other squamates except when forced onto the *D. punctatus* data (Table 2). The high rates of evolution required to yield the youngest date (*D. punctatus*; 1.49 Ma) exceed the rates of mitochondrial evolution known in squamates when forced onto the *C. bottae* complex and *L. zonata* data (Table 2). Consequently, although the placement of the genetic split between clades of *D. punctatus*, *E. multicarinata*, the *C. bottae* complex, and *L. zonata* roughly coincide, the temporal estimates of these genetic splits do not all match. Instead, it appears that at least two historical events in southern California may have influenced cladogenesis in the four codistributed taxa. The divergences between the northwestern and southern California clades of the *C. bottae* complex, and between the northern and southern California clades of *L. zonata*, appear to have occurred sometime in the Miocene/Pliocene. The splits between the northern and southern California *D. punctatus* lineages, and between the coastal and southern California subclades of *E. multicarinata*, may have occurred sometime in the Pliocene/Pleistocene.

Tree-mapping analyses

Except for one species comparison, the number of parallel divergence events shared between taxa is not distinguishable from the random distribution of codivergences. As such, we could not reject the null hypothesis that most species possess distinct branching histories (Table 3). However, the tree-mapping analysis of *E. multicarinata* and *L. zonata* recovers seven parallel divergence events, a degree of codivergence that appears nonrandom ($P = 0.0154$). The sequence of branching events between the southern California subclade of *E. multicarinata* and southern California clade of *L. zonata* is identical, and additional codivergence occurs between nodes of the northern California clades (Fig. 6). The tree-mapping analysis also shows several areas of incongruence between the *E. multicarinata* and *L. zonata* haplotype genealogies and proposes five events to explain such conflict: two sorting events and three instances of migration (Fig. 6). One incongruence is due to a difference in the southern Sierra Nevada (F) where the southern Sierra Nevada subclade of *E. multicarinata* resides but where the coastal subclade of *L. zonata* occurs. Another point of conflict results from a discrepancy in the Santa Cruz region (L), occupied by the northern California subclade of *E. multicarinata* but the coastal subclade of *L. zonata*. The last incongruence between *E. multicarinata* and *L. zonata* phylogenies is the imperfect branching order of northern California haplotypes. Despite these conflicts, *E. multicarinata* and *L. zonata* populations appear to have codiverged over the same landscape.

Demographic analyses

Four of the five woodland squamates show signatures of population stability in southern lineages but recent population expansions in relatively northern clades. The southernmost clades of *C. tenuis*, *D. punctatus*, *E. multicarinata*, and *L. zonata* contain the highest levels of genetic diversity (θ_p), normal F_S values, and corrected *g* values (Lessa *et al*.

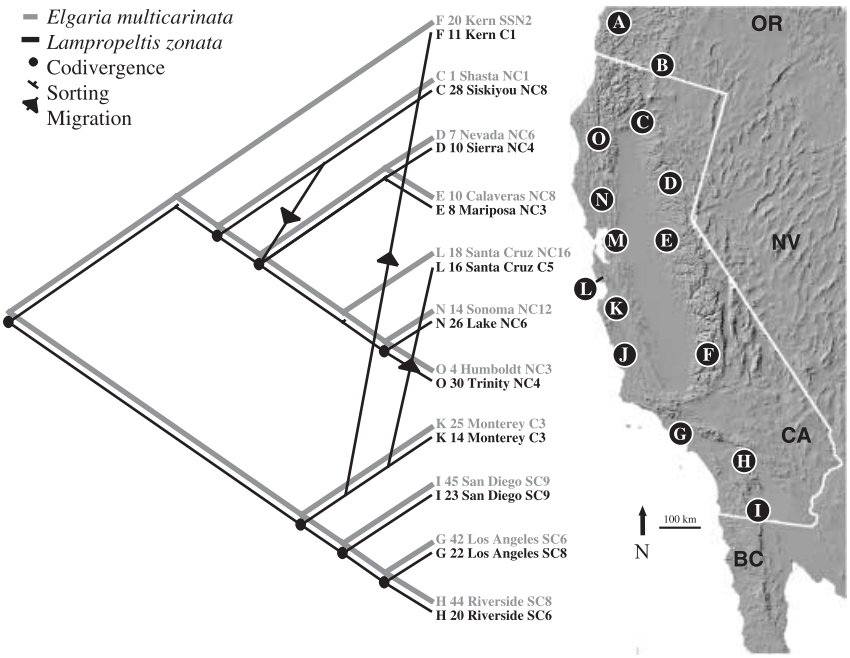

Fig. 6 Optimal reconciliation of *Lampropeltis zonata* phylogeography onto *Elgaria multicarinata* phylogeography. Tree-mapping analysis recovers seven parallel divergence events, a nonrandom degree of codivergence ($P = 0.0154$). The tree-mapping analysis also shows several areas of incongruence between *Elgaria multicarinata* and *Lampropeltis zonata* haplotype trees and proposes two sorting events and three migration events to explain such conflict. Reconciled trees are labelled with tree-map sample, sample number, county, and clade-specific haplotype. Tree-map samples refer to sample localities (A-O) used in the pruned tree-mapping analyses (Appendix) as shown on the map of southern Oregon (OR), California (CA), Nevada (NV), and northern Baja California (BC).

Table 4 Population growth estimates for regional mtDNA clades using both ML-based coalescent approach (g) and noncoalescent method (F_S), as well as nucleotide diversity estimates (θ_p). We considered g values significant if $g > 3$ SD (Lessa *et al*. 2003). Estimates of $g < 3$ SD were given a value of zero and indicate a lack of exponential population growth. Note that positive corrected g values, highly skewed F_S values, and low θ_p values generally correspond

Taxon Position: clade or subclade	Growth parameter (g)	SD of g	$g - 3$ SD (corrected g)	F_S	P value	θ_p	SD of θ_p
C. tenuis							
North: coastal clade	7150.180	2228.061	465.996	–1.387	0.048	0.929	0.809
South: interior/Sierra Nevada subclade	413.555	166.591	0	–2.018	0.185	5.275	2.989
D. punctatus							
North: northern California clade	526.035	151.829	70.549	–4.292	0.045	4.262	2.418
South: southern California clade	195.208	109.369	0	0.419	0.474	7.867	4.929
E. multicarinata							
North: northern California subclade	431.282	87.977	167.349	–6.540	0.004	8.346	4.535
Central: coastal subclade	77.967	54.840	0	–0.624	0.369	10.962	5.994
South: southern California subclade	142.036	50.029	0	–3.569	0.065	10.758	5.745
C. bottae complex							
North: northwestern subclade	32.506	25.801	0	3.199	0.909	19.154	10.205
Central: Sierra Nevada subclade	199.879	50.488	48.415	–3.459	0.072	9.614	5.154
South: southern California clade	1377.102	271.933	561.303	–2.084	0.062	5.200	3.382
L. zonata							
North: northern California subclade	308.836	66.474	109.422	–0.588	0.356	6.258	3.598
Central: coastal subclade	313.756	65.713	116.616	–2.183	0.077	10.500	6.108
South: southern California clade	117.761	34.275	14.936	–1.834	0.154	15.182	8.227

2003) that are 'insignificant' (Table 4). Conversely, the northernmost lineages of *C. tenuis*, *D. punctatus*, *E. multicarinata*, and *L. zonata* contain the lowest θ_p, highly skewed F_S values, and positive corrected g values (Table 4). Although the southern clade of *L. zonata* possesses a positive corrected g value, this estimate was an order of magnitude less than the same measure in the northern subclade. Additionally, the southern clade of *L. zonata* displays a normal F_S value and the highest level of nucleotide diversity measured among *L. zonata* lineages. Likewise, a highly skewed F_S in

the southern subclade of *E. multicarinata* is tempered by an insignificant estimate of *g* and a higher measure of molecular diversity in this group than in the northern subclade. Thus, the southernmost clades of *C. tenuis*, *D. punctatus*, *E. multicarinata*, and *L. zonata* display evidence of long-term population stability, while the northernmost lineages of these taxa exhibit signatures of rapid population growth. However, the demographic history of the *C. bottae* complex shows an opposite trend in genetic diversity and population structure. The southern most lineage of *C. bottae* complex exhibits the lowest θ_p, highly skewed F_S values, and positive corrected *g* values, while the northern most clade shows the reverse (Table 4). A closer examination of the northwestern subclade, however, suggests that population genetic structure and molecular diversity is greatest in central California, yet nearly absent in the more northern subgroups. Hence, more focused sampling and demographic analyses might show patterns of expansion in the northern range of the *C. bottae* complex consistent with other taxa. Taken together, these mtDNA data indicate concerted demographic responses in regional clades, with no or little expansion in southern lineages, but evidence of exponential increases in population growth in northern lineages.

Discussion

Deep genetic structure: vicariance in California squamates

Phylogenetic analyses of mtDNA variation in *Contia tenuis*, *Diadophis punctatus*, *Elgaria multicarinata*, the *Charina bottae* complex, and *Lampropeltis zonata* show that several taxa share geographical subdivisions. We can identify at least three areas where taxa share a major phyletic break in California (i) Transverse Ranges; (ii) Monterey Bay and Sacramento-San Joaquin Delta; and (iii) southern Sierra Nevada (Table 2). These geographical splits are roughly congruent across a number of sympatric species in this study and have also been recognized as genetic boundaries in other California taxa (Calsbeek *et al*. 2003).

When a genetic break is shared across codistributed species, we infer that the same vicariant event has similarly influenced the evolution of sympatric taxa (Wiley 1981; Brooks 1985; Brooks & McLennan 1991; Walker & Avise 1998; Arbogast & Kenagy 2001). Nevertheless, corresponding spatial structure between taxa may result from temporally independent vicariant events. To determine whether congruent genetic structure in these species has resulted from single or multiple events, we dated the divergences between major mtDNA clades. If the temporal component of concordant genetic subdivision matched, then we accepted the hypothesis that a single vicariant event has similarly structured taxa.

Four of the five taxa examined here display a major genetic split across the Transverse Ranges in southern California. Well-differentiated clades of *D. punctatus*, *E. multicarinata*, the *C. bottae* complex (Rodriguez-Robles *et al*. 2001), and *L. zonata* (Rodriguez-Robles *et al*. 1999) occur on either side of the Transverse Ranges. Southern California clearly contains the highest number of endemic lineages, yet our divergence estimates between clades divided by the Transverse Ranges vary (Table 2). Molecular divergences across the Transverse Ranges appear larger in the *C. bottae* complex (Rodriguez-Robles *et al*. 2001) and *L. zonata* (Rodriguez-Robles *et al*. 1999) than in *D. punctatus* or *E. multicarinata*. We estimated that the separation between the two deepest lineages of the *C. bottae* complex and *L. zonata* occurred sometime during the Miocene/Pliocene (5.31–3.33 Ma). Our molecular clock estimates for clades of *D. punctatus* and *E. multicarinata* divided by the Transverse Ranges suggest these lineages extend only into the Pliocene/Pleistocene (1.63–1.49 Ma). Here, we reject the hypothesis that congruent phyletic structure in *D. punctatus*, *E. multicarinata*, the *C. bottae* complex, and *L. zonata* has resulted from a single vicariant event along the Transverse Ranges because the rates of mtDNA evolution required to reconcile these dates falls outside those seen in squamates (Table 2). It appears that at least two historical events in southern California may have influenced cladeogenesis in these four codistributed taxa.

Rodriguez-Robles *et al*. (1999, 2001) hypothesized that Miocene/Pliocene marine incursions into the southern Coast Ranges may have fragmented populations of *L. zonata* and the *C. bottae* complex. However, the embayment of the Santa Maria Basin did not extend into the Great Central Valley (Dupré *et al*. 1991), so it is uncertain if this Pacific inundation would have entirely isolated populations north and south of the Transverse Ranges. An alternative hypothesis is that the uplift of the Transverse Ranges during the Miocene/Pliocene similarly shaped genetic diversity in the *C. bottae* complex and *L. zonata* (Calsbeek *et al*. 2003). It is unclear what historical events might account for the more recent division seen across the Transverse Ranges between clades of *D. punctatus* and *E. multicarinata*. Climatic fluctuations would have certainly changed the distribution of woodland habitat, perhaps isolating populations on separate slopes of the Transverse Ranges. The phylogeographical pattern displayed by *D. punctatus* of little genetic variation characterized by a single break across the Transverse Ranges is followed almost exactly in the deer mouse, *Peromyscus californicus* (Smith 1979), the titmouse, *Baeolophus inornatus* (Cicero 1996), and the thrasher, *Toxostoma redivivum* (Sgariglia & Burns 2003). Such a recurrent pattern suggests a parallel response to climatic or geological change.

The second congruent spilt occurs between key clades of *E. multicarinata* and *L. zonata* (Rodriguez-Robles *et al*. 1999)

on either side of the Monterey Bay and Sacramento-San Joaquin Delta. Our divergence estimates suggest the split between *E. multicarinata* and *L. zonata* clades currently divided by the Monterey Bay and Sacramento-San Joaquin Delta occurred over 4 Ma and 3 Ma, respectively (Table 2). Stratigraphic and other geological evidence indicate the Pacific Ocean invaded interior California through present-day Monterey Bay sometime during the late Pliocene until the mid-Pleistocene (DuprÈ 1990). Concomitant with the retreat of the Monterey seaway was the formation of the Sacramento-San Joaquin Delta through the San Francisco Bay during the mid-Pleistocene (Duprè *et al*. 1991). The marine embayment is thought to have played a crucial role in the diversification of the salamander *Ensatina* in this region (Wake 1997) while the more recent Sacramento-San Joaquin Delta is considered to have separated populations of *Thomomys bottae* (Patton & Smith 1990), *L. zonata* (Rodriguez-Robles *et al*. 1999), and *Neotoma fuscipes* (Matocq 2002a). The degree of congruence between these independent phylogeographies and the historical Monterey embayment and Sacramento-San Joaquin Delta suggests that these long–standing barriers may have played an important role in regional cladogenesis.

Finally, we identified congruent subdivision in the southern Sierra Nevada, which possesses distinct mitochondrial breaks in *C. tenuis*, and *E. multicarinata*. This region is characterized by three impressive drainages: the Kings, Kaweah, and Kern Rivers. The largest of these is the Kern River, which cuts nearly 2700 m into the Sierra Nevada and has a tectonic and glacial past (Whitney 1979). The Kern River Canyon is particularly arid and is thought to be an important barrier to *Batrachoseps* movement (Jockusch *et al*. 1998; Jockusch & Wake 2002). Our molecular clock estimates suggest that the southern Sierra Nevada subclades of *C. tenuis* and *E. multicarinata* separated approximately 2 Ma from their respective sister groups. These dates correspond roughly with the onset of glaciation in the major drainages of the Sierra Nevada (Guyton 1998).

Shared phyletic breaks across the Transverse Ranges, Monterey Bay and the Sacramento-San Joaquin Delta, and the southern Sierra Nevada, suggest that vicariance may have driven cladogenesis in these California taxa. Here, similar genetic discontinuities timed across squamate lineages generally correspond to known historical events. Thus, past geological and climatic events appear to have been important in shaping diversity in *C. tenuis*, *D. punctatus*, *E. multicarinata*, the *C. bottae* complex, and *L. zonata*. However, we show that congruence in the spatial arrangement of genetic structure sometimes results from temporally independent vicariant events. An additional complication, in our case, is the ring-like distribution of suitable habitat around the Great Central Valley in California. This unique distribution confounds our ability to establish and date specific vicariant events because clades often meet in two locations, giving the appearance of two genetic breaks. We assume that in instances where clades meet in two places, one area is the location where an initial vicariant event occurred, and the other a zone of secondary contact (e.g. *E. multicarinata*; Fig. 5). Future work in California should approach this challenge with more detailed molecular and morphological data (e.g. Matocq 2002b).

Codivergence: concerted fragmentation and colonization

At a gross level, deep genetic structure in *C. tenuis*, *D. punctatus*, *E. multicarinata*, the *C. bottae* complex, and *L. zonata* often coincides both spatially and temporally. Comparing the placement and timing of major genetic divergences across taxa is useful in isolating instances of shared vicariance and in identifying the potential causal agents of such vicariance. However, a more comprehensive approach would not only compare geographical splits between codistributed taxa, but contrast entire phylogenetic topologies between separate species. If the sequence of branching events is congruent among sympatric taxa, then the entire succession of vicariance and dispersal events in those species must have progressed together in lock-step fashion through time (Sullivan *et al*. 2000). We might expect such topological congruence if sympatric taxa have similar abiotic and biotic requirements and have occupied the same communities through time (Sullivan *et al*. 2000).

We compared the degree of shared phyletic history exhibited between codistributed species via tree-mapping (Page 1994a, b). Here, only *E. multicarinata* and *L. zonata* demonstrate an overall concerted response through time, exhibiting seven parallel divergence events over the same landscape (Table 3). The sequence of branching events between the southern California subclade of *E. multicarinata* and southern California clade of *L. zonata* is identical, and additional codivergence occurs between nodes of the northern California clades (Fig. 6). Thus, the coincidental way that *E. multicarinata* and *L. zonata* clades are hierarchically nested suggests that the progression of fragmentation and colonization in these species occurred in concert. We also infer that *E. multicarinata* and *L. zonata* have been residents of the same communities throughout their histories. Today these species commonly share specific microhabitats (Stebbins 2003). In fact, *L. zonata* is known to prey on *E. multicarinata* (Parham & Feldman 2003), suggesting that these reptiles are not simply members of the same communities, but may be direct ecological associates.

However, topological agreement between *E. multicarinata* and *L. zonata* phylogeographies is not perfect; there is incongruence in the southern Sierra Nevada, the Santa Cruz region, and in northern California (Fig. 6). Furthermore, phylogeographical comparison via tree mapping shows that significant structure is not shared between the other squamate taxa (Table 3). Here, differences between

phylogeographies may result from uneven sampling efforts, unique dispersal events (Page 1994b), random lineage sorting (Page 1994b), disparity in residence times, or incorrect phylogeny estimation (Johnson *et al*. 2001). Due to these factors, species-specific phylogeographical patterns may be common in comparative phylogeographical studies.

Demographic history

In addition to sharing the spatial and temporal arrangement of major genetic breaks, as well as congruence in finer-scale branching patterns, taxa responding similarly to historical events should exhibit similar patterns of historical demography. Thus, we were also interested in historical patterns that have arisen recently within lineages. Given the climatic history of western North America, we can make specific predictions about the demographic patterns expected in these species. Holocene warming trends have reduced woodland habitat that was more widespread in southern California, including portions of the Mojave Desert, while at the same time increasing available habitat in the North (Van Devender & Spaulding 1979; Smith *et al*. 2000). The genetic signature of a range expansion should result from rapid 'pioneer' colonization of newly available habitat (Nichols & Hewitt 1994; Hewitt 2000). As such, demographic patterns within each taxon should display a relative increase in population growth moving from south to north.

Both coalescent and noncoalescent estimates of population expansion, as well as a measure of nucleotide diversity, indicate that populations in more southern clades studied here have been stable, while populations in more northern clades have recently expanded. The more southerly clades of *C. tenuis*, *D. punctatus*, *E. multicarinata*, and *L. zonata* show greater nucleotide diversity and evidence of no or limited population growth (Table 4). Conversely, the more northern lineages of *C. tenuis*, *D. punctatus*, *E. multicarinata*, and *L. zonata* display less genetic diversity and evidence of exponential increases in population growth (Table 4). A pattern of long-term population stability in southern or central California and rapid population growth in northern California and Oregon has also been demonstrated in other woodland vertebrates (Matocq 2002a; Kuchta & Tan 2005; Spinks & Shaffer 2005).

Conclusions

A number of the squamate reptiles examined here share spatially and temporally concordant phyletic breaks in California. These shared patterns suggest that historical events have been important in shaping gross genetic patterns in these taxa. However, at least one shared phylogeographical break does not appear temporally concordant. Such 'false' concordance might be common in areas that have undergone repeated historical events (e.g. glacial cycles), yielding matching spatial patterns, but from temporally independent vicariant episodes (Matocq 2002a). Likewise, more recent demographic patterns suggest that these woodland reptiles have expanded into areas that became available as Holocene warming allowed the spread of suitable habitat into northern California and Oregon. Despite coarse-scale congruence in both deeper phylogeographical structure and more recent demographic trends, only two taxa possess matching branching patterns. In spite of explicitly limiting the scope of our study to closely related taxa that occupy similar trophic levels with ecological requirements, unique genetic patterns have evolved over the same landscape. Here only *E. multicarinata* and *L. zonata* share significant codivergences, indicative of long-term association with the same community and possibly each other. Future phylogeographical studies of these two taxa may lead to added insight into the precise ecological and evolutionary processes that resulted in current patterns of diversity in these woodland organisms.

Acknowledgements

For providing tissue sample critical to this study we thank: Ted Papenfuss, Harry Greene, Dave Wake, Carla Cicero (MVZ); Jens Vindum, Michelle Koo, Bob Drewes (CAS); Bob Macey; Dan Mulcahy; Jim Parham; Brad Shaffer; Bob Hansen; Richard Hoyer; Robert Fisher; Jon Richmond; Dave Kizirian, Kent Beaman (LACM); Clark Mahrdt (SDSNH); William Rader; Norm Scott; Walt Sakai; Shawn Kuchta; Emily Taylor; Kris Lapin; Jim Buskirk; Tod Reeder (SDSU); Kirk Setser; Jon Campbell (UTACV). We thank Marjorie Matocq, Ted Papenfuss, Dan Mulcahy, Jim Parham, Mike Pfrender, Javier Rodriguez-Robles, Eric O'Neill, Eric Routman, Harry Greene, and the USU herp group for useful comments, suggestions, and tireless support. We appreciate field assistance from Dan Mulcahy, Jim Parham and Marjorie Matocq, and permits from the California Department of Fish and Game. We are grateful to Craig Reading, Karen Holder, Frank Cipriano, and Marjorie Matocq for lab assistance. Finally, we thank Wolfgang Wüster for assistance with molecular clock estimation and comments from two anonymous reviewers. This work was supported by a Sigma Xi Grants-in-Aid to CRF, a United States Department of Education GAANN fellowship to CRF, a National Science Foundation grant DEB-9629546 to GSS and a National Institutes of Health MBRS scores 5 grant GM52588 to GSS.

References

Arbogast BS, Kenagy GJ (2001) Comparative phylogeography as an integrative approach to historical biogeography. *Journal of Biogeography*, **28**, 819–825.

Arevalo E, Davis SK, Sites JW (1994) Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. *Systematic Biology*, **43**, 387–418.

Avise JC (1989) Gene trees and organismal histories: a phylogenetic approach to population biology. *Evolution*, **43**, 1192–1208.

Avise JC, Arnold J, Ball R *et al.* (1987) Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, **18**, 489–522.

Blanchard FN (1942) The ringneck snakes, genus *Diadophis*. *Bulletin of the Chicago Academy of Sciences*, **7**, 1–144.

Bremer K (1994) Branch support and tree stability. *Cladistics*, **10**, 295–304.

Brooks DR (1985) Historical ecology: a new approach to studying the evolution of ecological associations. *Annals of the Missouri Botanical Garden*, **72**, 660–680.

Brooks DR, McLennan DA (1991) *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology*. The University of Chicago Press, Chicago, Illinois.

Brown JH, Lomolino MV (1998) *Biogeography*, 2nd edn. Sinauer Associates, Sunderland, Massachusetts.

Cadle JE (1984) Molecular systematics of Neotropical xenodontine snakes. III. Overview of xenodontine phylogeny and the history of New World snakes. *Copeia*, **1984**, 641–652.

Calsbeek R, Thompson JN, Richardson JE (2003) Patterns of molecular evolution and diversification in a biodiversity hotspot: the California Floristic Province. *Molecular Ecology*, **12**, 1021–1029.

Cicero C (1996) *Sibling Species of Titmice in the* Parus inornatus *Complex (Aves: Paridae)*. University of California Press, Berkeley, California.

DupréWR (1990) Quaternary geology of the Monterey Bay region, California. In: *Geology and Tectonics of the Central California Coast Region, San Francisco to Monterey* (ed. Garrison RE), pp. 185–191. Society of Economic Paleontology and Mineralogy, Pacific Section, Bakersfield, California.

DuprÈWR, Morrison RB, Clifton HE *et al.* (1991) Quaternary geology of the Pacific margin. In: *The Geology of North America. Quaternary Nonglacial Geology: Conterminous U.S.* (ed. Morrison RB), pp. 141–214. Geology Society of America, Boulder, Colorado.

Farris JS (1983) The logical basis of phylogenetic analysis. In: *Advances in Cladistics* (ed. Platnick N Funk VA), pp. 7–36. Columbia University Press, New York, New York.

Feldman CR, Spicer GS (2002) Mitochondrial variation in sharp-tailed snakes (*Contia tenuis*): evidence of a cryptic species. *Journal of Herpetology*, **36**, 648–655.

Felsenstein J (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution*, **17**, 368–376.

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**, 783–791.

Felsenstein J (1993) PHYLIP *(Phylogenetic Inference Package)*. Department of Genetics. University of Washington, Seattle, Washington.

Fu Y-X (1997) Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics*, **147**, 915–925.

Goldman N (1993) Statistical tests of models of DNA substitution. *Journal of Molecular Evolution*, **63**, 182–198.

Good DA (1988a) Phylogenetic relationships among gerrhonotine lizards: an analysis of external morphology. *University of California Publications in Zoology*, **121**, 1–139.

Good DA (1988b) Allozyme variation and phylogenetic relationships among the species of *Elgaria* (Squamata: Anguidae). *Herpetologica*, **44**, 154–162.

Graur D, Martin W (2004) Reading the entrails of chickens: molecular timescales of evolution and the illusion of precision. *Trends in Genetics*, **20**, 80–86.

Guyton B (1998) *Glaciers of California: Modern Glaciers, Ice Age Glaciers, Origin of Yosemite Valley, and a Glacier Tour in the Sierra Nevada*. University of California Press, Berkeley, California.

Hasegawa M, Kishino K, Yano T (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, **21**, 160–174.

Hewitt GM (2000) The genetic legacy of the Quaternary ice ages. *Nature*, **405**, 907–913.

Hillis DM, Bull JJ (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology*, **42**, 182–192.

Hillis DM, Mable BK, Moritz C (1996) Applications of molecular systematics: the state of the field and a look to the future. In: *Molecular Systematics* (eds Hillis DM Moritz C Mable BK), pp. 515–543. Sinauer Associates, Sunderland, Massachusetts.

Hoyer RF (2001) Discovery of a probable new species in the genus *Contia*. *Northwest Naturalist*, **82**, 116–122.

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**, 754–755.

Jockusch EL, Wake DB (2002) Falling apart and merging: diversification of slender salamanders (Plethodontidae: *Batrachoseps*) in the American West. *Biological Journal of the Linnaean Society*, **76**, 361–391.

Jockusch EL, Wake DB, Yanev KP (1998) New species of slender salamanders, *Batrachoseps* (Amphibia: Plethodontidae), from the Sierra Nevada of California. *Natural History Museum of Los Angeles County Science Series*, **472**, 1–17.

Johnson KP, Drown DM, Clayton DH (2001) A data based parsimony method of cophylogenetic analysis. *Zoologica Scripta*, **30**, 79–87.

Kimura M (1980) A simple method for estimating evolutionary rate of base pair substitution through comparative studies of nucleotide sequence. *Journal of Molecular Evolution*, **16**, 111–120.

Kuchta SR, Tan AM (2005) Isolation by distance and post-glacial range expansion in the rough-skinned newt, *Taricha granulosa*. *Molecular Ecology*, **14**, 225–244.

Kuhner MK, Yamato J, Felsenstein J (1995) Estimating effective population size and mutation rate from sequence data using Metropolis–Hastings sampling. *Genetics*, **140**, 1421–1430.

Kuhner MK, Yamato J, Felsenstein J (1998) Maximum likelihood estimation of population growth rates based on the coalescent. *Genetics*, **149**, 429–434.

Kumazawa Y, Nishida M (1993) Sequence evolution of mitochondrial tRNA genes and deep-branch animal phylogenetics. *Journal of Molecular Evolution*, **37**, 380–398.

Kumazawa Y, Nishida M (1995) Variations in mitochondrial tRNA gene organization of reptiles as phylogenetic markers. *Molecular Biology and Evolution*, **12**, 759–772.

Kumazawa Y, Ota H, Nishida M, Ozawa T (1996) Gene rearrangements in snake mitochondrial genomes: highly concerted evolution of control-region-like sequences duplicated and inserted into a tRNA gene center. *Molecular Biology and Evolution*, **13**, 1242–1254.

Lais MP (1976) *Gerrhonotus multicarinatus* (Blanville), southern alligator lizard. *Catalogue of American Amphibians and Reptiles*, **187**, 187.181–187.187.184.

Langley CH, Fitch WM (1974) An estimation of the constancy of the rate of molecular evolution. *Journal of Molecular Evolution*, **3**, 161–177.

Lapointe FJ, Rissler LJ (2005) Congruence, consensus, and the comparative phylogeography of codistributed species in California. *American Naturalist*, **166**, 290–299.

Larget B, Simon DL (1999) Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. *Molecular Biology and Evolution*, **16**, 750–759.

Leaché AD, Reeder TW (2002) Molecular systematics of the Eastern Fence Lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. *Systematic Biology*, **51**, 44–68.

Leonard WP, Ovaska K (1998) Contia, C. tenuis. *Catalogue of American Amphibians and Reptiles*, **677**, 671–677,677.

Lessa EP, Cook JA, Patton JL (2003) Genetic footprints of demographic expansion in North America, but not Amazonia, during the Late Quaternary. *Proceedings of the National Academy of Sciences, USA*, **100**, 10331–10334.

Macey JR, Verma A (1997) Homology in phylogenetic analysis: alignment of transfer RNA genes and the phylogenetic position of snakes. *Molecular Phylogenetics and Evolution*, **7**, 272–279.

Macey JR, Larson A, Ananjeva NB, Fang Z, Papenfuss TJ (1997) Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution*, **14**, 91–104.

Macey JR, Schulte JAII, Larson A *et al.* (1999) Molecular phylogenetics, tRNA evolution, and historical biogeography in anguid lizards and related taxonomic families. *Molecular Phylogenetics and Evolution*, **12**, 250–272.

Maddison DR, Maddison WP (2000) MACCLADE: *Analysis of Phylogeny and Character Evolution*. Sinauer, Sunderland, Massachusetts.

Maddison WP, Donoghue MJ, Maddison DR (1984) Outgroup analysis and parsimony. *Systematic Zoology*, **33**, 83–103.

Mahoney MJ (2004) Molecular systematics and phylogeography of the *Plethodon elongatus* species group: combining phylogenetic and population genetic methods to investigate species history. *Molecular Ecology*, **13**, 149–166.

Maniatis T, Fristch EF, Sambrook J (1982) *Molecular Cloning: A Laboratory Manual*. Cold Spring Harbor Publication, Cold Spring Harbor, New York.

Matocq MD (2002a) Phylogeographical structure and regional history of the dusky-footed woodrat, *Neotoma fuscipes*. *Molecular Ecology*, **11**, 229–242.

Matocq MD (2002b) Morphological and molecular analysis of a contact zone in the *Neotoma fuscipes* species complex. *Journal of Mammalogy*, **83**, 866–883.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Nichols RA, Hewitt GM (1994) The genetic consequences of long distance dispersal during colonisation. *Heredity*, **72**, 312–317.

Page RDM (1994a) Parallel phylogenies: reconstructing the history of host-parasite assemblages. *Cladistics*, **10**, 155–173.

Page RDM (1994b) Maps between trees and cladistic analysis of historical associations among genes, organisms, and areas. *Systematic Biology*, **43**, 58–77.

Parham JF, Feldman CR (2003) *Lampropeltis zonata*. Diet. *Herpetological Review*, **34**, 150.

Patton JL, Smith MF (1990) The evolutionary dynamics of the pocket gopher *Thomomys bottae*, with emphasis on California populations. *University of California Publications in Zoology*, **123**, 161.

Pinou T, Vicario S, Marschner M, Caccone A (2004) Relict snakes of North America and their relationships within Caenophidia, using likelihood-based Bayesian methods on mitochondrial sequences. *Molecular Phylogenetics and Evolution*, **32**, 563–574.

Posada D, Crandall KA (1998) MODELTEST: testing the model of DNA substitution. *Bioinformatics*, **14**, 817–818.

Rannala B, Yang ZH (1996) Probability distribution of molecular evolutionary trees: a new method of phylogenetic inference. *Journal of Molecular Evolution*, **43**, 304–311.

Richmond JQ, Reeder TW (2002) Evidence for parallel ecological speciation in scincid lizards of the *Eumeces skiltonianus* species group (Squamata: Scincidae). *Evolution*, **56**, 1498–1513.

Riddle BR, Hafner DJ, Alexander LF (2000) Comparative phylogeography of Baileys' pocket mouse (*Chaetodipus baileyi*) and the *Peromyscus eremicus* species group: historical vicariance of the Baja California peninsular desert. *Molecular Phylogenetics and Evolution*, **17**, 161–172.

Robinson-Rechavi M, Huchon D (2000) RRTREE: Relative rates tests between groups of sequences on a phylogenetic tree. *Bioinformatics*, **16**, 296–297.

Rodriguez-Robles JA, Denardo DF, Staub RE (1999) Phylogeography of the California mountain kingsnake, *Lampropeltis zonata* (Colubridae). *Molecular Ecology*, **8**, 1923–1934.

Rodriguez-Robles JA, Stewart GR, Papenfuss TJ (2001) Mitochondrial DNA-based phylogeography of North American rubber boas, *Charina bottae* (Serpentes: Boidae). *Molecular Phylogenetics and Evolution*, **18**, 227–237.

Saiki RK, Gelfand DH, Stoffel S *et al.* (1988) Primer directed enzymatic amplification of DNA with a thermostable DNA polymerase. *Science*, **239**, 487–491.

Sanger F, Nicklen S, Coulson AR (1977) DNA sequencing with chain-terminating inhibitors. *Proceedings of the National Academy of Sciences, USA*, **74**, 5463–5467.

Sarich VM, Wilson AC (1973) Generation time and genomic evolution in primates. *Science*, **179**, 1144–1147.

Schneider S, Keuffer J-M, Roessli D, Excoffier L (2000) ARLEQUIN: *A Software Package for Population Genetics*. Genetics and Biometry Laboratory. University of Geneva, Geneva, Switzerland.

Schoenherr AA (1992) *A Natural History of California*. University of California Press, Berkeley, California.

Sgariglia EA, Burns KJ (2003) Phylogeography of the California Thrasher (*Toxostoma redivivum*) based on nested-clade analysis of mitochondrial DNA variation. *The Auk*, **120**, 346–361.

Smith MF (1979) Geographic variation in genic and morphological characters in *Peromyscus californicus*. *Journal of Mammalogy*, **60**, 705–722.

Smith FA, Matocq MD, Melendez KE, Ditto AM, Kelly PA (2000) How isolated are Pleistocene refugia? Results from a study on a relict woodrat population from the Mojave Desert, California. *Journal of Biogeography*, **27**, 483–500.

Sorenson MD (1999) TREEROT. Boston University, Boston, Massachusetts.

Spinks PQ, Shaffer HB (2005) Range-wide molecular analysis of the western pond turtle (*Emys marmorata*): cryptic variation, isolation by distance, and their conservation implications. *Molecular Ecology*, **14**, 2047–2064.

Stebbins RC (2003) *A Field Guide to the Western Reptiles and Amphibians*., 3rd edn. Houghton Mifflin Co, Boston, Massachusetts.

Sullivan J, Arellano E, Rogers DS (2000) Comparative phylogeography of Mesoamerican highland rodents: concerted versus independent response to past climate fluctuations. *American Naturalist*, **155**, 755–768.

Swofford DL (2002) PAUP*: *Phylogenetic analysis using parsimony (*and other methods)*. Sinauer Associates Inc, Sunderland, Massachusetts.

van Tuinen M, Hedges SB (2001) Calibration of avian molecular clocks. *Molecular Biology and Evolution*, **18**, 206–213.

Van Devender TR, Spaulding WG (1979) Development of vegetation and climate in the southwestern United States. *Science*, **204**, 701–710.

Vidal N, Kindl SK, Wong A, Hedges SB (2000) Phylogenetic relationships of xenodontine snakes inferred from 12S and 16S ribosomal RNA sequences. *Molecular Phylogenetics and Evolution*, **14**, 389–402.

Wake DB (1997) Incipient species formation in salamanders of the *Ensatina* complex. *Proceedings of the National Academy of Sciences, USA*, **94**, 7761–7767.

Walker D, Avise JC (1998) Principles of phylogeography as illustrated by freshwater and terrestrial turtles in the southeastern United States. *Annual Review of Ecology and Systematics*, **29**, 23–58.

Wares JP, Cunningham CW (2001) Phylogeography and historical ecology of the North Atlantic intertidal. *Evolution*, **55**, 2455–2469.

Watterson GA (1975) On the number of segregating sites in genetical models without recombination. *Theoretical Population Biology*, **7**, 256–276.

Whitney S (1979) *A Sierra Club Naturalist's Guide to the Sierra Nevada*. Sierra Club Books, San Francisco, California.

Wiley EO (1981) *Phylogenetics: the Theory and Practice of Phylogenetic Systematics*. John Wiley & Sons Inc., New York, New York.

Wu CI, Li W-H (1985) Evidence for higher rates of nucleotide substitution in rodents than in man. *Proceedings of the National Academy of Sciences*, **82**, 1741–1745.

Wüster W, Ferguson JE, Quijada-Mascarenas JA *et al.* (2005) Tracing an invasion: landbridges, refugia, and the phylogeography of the Neotropical rattlesnake (Serpentes: Viperidae: *Crotalus durissus*). *Molecular Ecology*, **14**, 1095–1108.

Yang Z (1994a) Estimating patterns of nucleotide substitution. *Journal of Molecular Evolution*, **39**, 105–111.

Yang Z (1994b) Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. *Journal of Molecular Evolution*, **39**, 306–314.

Yang Z (1996) Maximum likelihood models for combined analyses of multiple sequence data. *Journal of Molecular Evolution*, **42**, 587–596.

Zaher H (1999) Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic xenodontinae and a reappraisal of colubroid hemipenes. *Bulletin of the American Museum of Natural History*, 1–168.

Zink RM (2002) Methods in comparative phylogeography, and their application to studying evolution in the North American aridlands. *Integrative and Comparative Biology*, **42**, 953–959.

Chris R. Feldman is currently a PhD student at Utah State University examining adaptive genetic variation in garter snakes (*Thamnophis*). Chris is interested in a broad range of evolutionary questions and conservation issues in reptiles, and this study represents his Master's research under the guidance of Greg S. Spicer. Greg is an associate professor at San Francisco State University whose lab tackles a host of molecular systematic topics, from cospeciation between birds and their parasites, to issues of phylogenetic theory. Chris is a lifelong Oakland Raiders fan. Greg is very tall.

Appendix

Unique *Contia tenuis*, *Diadophis punctatus*, *Elgaria multicarinata*, *Elgaria panamintina*, *Elgaria paucicarinata*, *Elgaria kingii* and outgroup samples, mtDNA haplotypes, general localities, museum vouchers and GenBank Accession nos. CAS, California Academy of Sciences; MVZ, Museum of Vertebrate Zoology; LSUMZ, Louisiana State University Museum of Natural Science; LACM, Los Angeles County Museum of Natural History; SDSU, San Diego State University; SDSNH, San Diego Natural History Museum; UTACV, University of Texas, Arlington; CRF, C.R. Feldman (deposited at CAS); HBS, H.B. Shaffer; RFH, Richard F. Hoyer (measured and released); RM, J.R. Macey. *Charina bottae* and *Lampropeltis zonata* are from Rodriguez-Robles *et al*. (2001, 1999) and follow the above abbreviations with some additions: CSPU, California State Polytechnic University, Pomona; HWG, H.W. Greene (deposited at MVZ); RES, R.E. Staub; SJA, S.J. Arnold

Taxon	Sample no.	TreeMap locality	Haplotype no.	General locality, county, and state	Specimen no. GenBank no.
Contia tenuis					
C. tenuis	1	B	I/SN1	S. of Emigrant Lake, Jackson Co., OR	RFH 1el; AF258879
C. tenuis	2		′	Hilt, Siskiyou Co., CA	CAS 210367; AF258879
C. tenuis	3	C	I/SN2	Potter Creek, Shasta Co., CA	MVZ 164926; AF258880
C. tenuis	4		I/SN3	Pike City, Sierra Co., CA	CAS 207044; AF402656
C. tenuis	5	D	′	Golden Trout, Butte Co., CA	CAS 205639; AF402656
C. tenuis	6		I/SN4	Golden Trout, Butte Co., CA	CAS 205652; AF258881
C. tenuis	7	E	I/SN5	S. of Georgetown, El Dorado Co., CA	CAS 208587; AF258882
C. tenuis	8		′	Rocklin, Placer Co., CA	CAS 210366; AF258882
C. tenuis	9		′	Chumash Circle, Calaveras Co., CA	MVZ 230096; AF258882
C. tenuis	10		′	Brittan Ranch, Glenn Co., CA	CAS 202582; AF258882
C. tenuis	11		′	Hwy 198, W. of Fresno Co. line, Monterey Co., CA	MVZ 208157; AF258882
C. tenuis	12		I/SN6	Bear Valley, Mariposa Co., CA	CAS 205778; AF258883
C. tenuis	13	J	I/SN7	Vineyard Drive, San Luis Obispo Co., CA	MVZ 208158; AF258884
C. tenuis	14		′	Vineyard Drive, San Luis Obispo Co., CA	MVZ 208160; AF258884
C. tenuis	15	K	I/SN8	Hastings University Calif. Reserve, Monterey Co., CA	CAS 205788; AF258885
C. tenuis	16	M	I/SN9	Pleasant Hill, Contra Costa Co., CA	MVZ 232671; AF258886
C. tenuis	17	N	I/SN10	Cache Creek, Yolo Co., CA	CAS 214873; AF402657
C. tenuis	18		I/SN11	Bolinas, Marin Co., CA	RFH 13 ca17; DQ364663
C. tenuis	19		SSN1	South Fork Tule River, Slate Mountain, Tulare Co., CA	CAS 224886; DQ364664
C. tenuis	20	F	SSN2	Trail of 100 Giants, Tulare Co., CA	RFH 13 ca13; DQ364665
C. tenuis	21		′	Trail of 100 Giants, Tulare Co., CA	RFH 13 ca14; DQ364665
C. tenuis	22	L	C1	China Grade Road, Santa Cruz Co., CA	CAS 205802; AF258887
C. tenuis	23		C2	Hwy 1 and 128 jct., Mendocino Co., CA	CAS 231505; AF258888
C. tenuis	24		′	Angelo Coast University Calif. Reserve, Mendocino Co., CA	MVZ 230270; AF258888
C. tenuis	25	O	′	NE. of Salyer, Trinity Co., CA	CAS 221864; AF258888
C. tenuis	26	A	′	W. of Glendale, Douglas Co., OR	CAS 224216; AF258888
C. tenuis	27		C3	Jackson State Forest, Mendocino Co., CA	MVZ 232650; AF402658
C. tenuis	28		′	Jackson State Forest, Mendocino Co., CA	MVZ 232651; AF402658
C. tenuis	29	†	C4	Carlotta, Humboldt Co., CA	CAS 221861; DQ364666
Diadophis punctatus					
D. p. occidentalis	1		NC1	Wren, Benton Co., OR	LSUMZ 83379; AF25889
D. p. occidentalis	2	A	′	W. of Glendale, Douglas Co., OR	LSUMZ 83380; AF25889
D. p. occidentalis	3	O	′	Willow Creek, Humboldt Co., CA	LSUMZ 83373; AF25889
D. p. occidentalis	4		′	Pepperwood CAS Reserve, Sonoma Co., CA	LSUMZ 83383; AF25889

Appendix *Continued*

Taxon	Sample no.	TreeMap locality	Haplotype no.	General locality, county, and state	Specimen no. GenBank no.
D. p. occidentalis	5	N	’	Quail Ridge University Calif. Reserve, Napa Co., CA	HBS 20027; AF25889
D. p. amabilis	6		’	Point Pinole, Contra Costa Co., CA	MVZ 229671; AF25889
D. p. amabilis	7	M	’	Briones Reservoir, Contra Costa Co., CA	LSUMZ 83377; AF25889
D. p. amabilis	8		’	Crystal Springs, San Mateo Co., CA	CAS 204287; AF25889
D. p. amabilis	9		’	San Bruno Mountain, San Mateo Co., CA	CAS 204258; AF25889
D. p. amabilis	10	L	’	Empire Grade Road, Santa Cruz Co., CA	HBS 16032; AF25889
D. p. vandenburghi	11		’	Corral de la Tierra Road, Monterey Co., CA	CAS 210365; AF25889
D. p. pulchellus	12		’	Placerville, El Dorado Co., CA	MVZ 180366; AF25889
D. p. pulchellus	13		’	E. of Wilseyville, Calaveras Co., CA	MVZ 228329; AF25889
D. p. pulchellus	14	F	’	Elderwood, Tulare Co., CA	MVZ 137856; AF25889
D. p. occidentalis	15	C	NC2	Mountain Gate, Shasta Co., CA	MVZ 229696; AF258890
D. p. occidentalis	16		’	Whiskeytown, Shasta Co., CA	HBS 15744; AF258890
D. p. occidentalis	17		NC3	Comptche, Mendocino Co., CA	LSUMZ 83382; AF258891
D. p. occidentalis	18		NC4	Cordelia, Solano Co., CA	MVZ 229697; AF258892
D. p. pulchellus	19	D	NC5	Jack Creek, Butte Co., CA	CAS 205831; AF258893
D. p. pulchellus	20		’	Kanaka Creek Drainage, Sierra Co., CA	CAS 203485; AF258893
D. p. pulchellus	21	E	NC6	Wilseyville, Calaveras Co., CA	MVZ 228328; AF258894
D. p. pulchellus	22		NC7	Petersen Mill Road, Fresno Co., CA	CAS 208804; AF258895
D. p. pulchellus	23		NC8	Camp Wishon, Tulare Co., CA	MVZ 229140; AF258896
D. p. amabilis	24		NC9	Novato, Marin Co., CA	MVZ 229674; AF258897
D. p. amabilis	25		NC10	Sunol, Alameda Co., CA	LSUMZ 83375; AF258898
D. p. vandenburghi	26	K	NC11	Hastings University Calif. Reserve, Monterey Co., CA	CRF 266; AF258899
D. p. amabilis	27		NC12	Pacheco Pass, Santa Clara Co., CA	SDSU 3935; AF258900
D. p. vandenburghi	28		’	Pinnacles National Monument, San Benito Co., CA	MVZ 228331; AF258900
D. p. vandenburghi	29	J	NC13	San Simeon, San Luis Obispo Co., CA	CAS 210425; AF258901
D. p. vandenburghi	30		NC14	Stoney Creek, San Luis Obispo Co., CA	CAS 208518; AF258902
D. p. modestus	31	G	NC15	Malibu Creek, Los Angeles Co., CA	LSUMZ 83374; AF258903
D. p. modestus	32		SC1	Santa Catalina Island, Los Angeles Co., CA	LACM 145522; AF258904
D. p. modestus	33		SC2	Telegraph Canyon, Orange Co., CA	no voucher; AF258905
D. p. modestus	34	H	SC3	James University Calif. Reserve, Riverside Co., CA	CAS 218661; AF258906
D. p. similis	35		SC4	Palomar Mountain, San Diego Co., CA	SDSNH 68750; AF258907
D. p. similis	36		SC5	Little Cedar, San Diego Co., CA	no voucher; AF258908
D. p. similis	37	I		Camp Pendalton, San Diego Co., CA	no voucher; AF258908
D. p. regalis	38			Clark Mountain, San Bernardino Co., CA	SDSNH 68893; DQ364667
D. p. regalis	39			Chiricahua Mountains, Cochise Co., AZ	MVZ 229665; AF258909
D. p. punctatus	40			Ochlok, Liberty Co., FL	CAS 203091; AF258910
Heterodon platirhinos				Southern Pines, Moore Co., NC	MVZ 175928; AF402659
Elgaria multicarinata					
E. m. scincicauda	1	C	NC1	Potter Creek, Shasta Co., CA	MVZ 150176; AF258911
E. m. scincicauda	2		’	Brook Creek, Shasta Co., CA	MVZ 162053; AF258911
E. m. scincicauda	3		NC2	Paynes Creek, Tehama Co., CA	CAS 206459; AF258912
E. m. scincicauda	4	O	NC3	Alderpoint, Humboldt Co., CA	MVZ 162062; AF258913
E. m. multicarinata	5		NC4	E. of Jack Creek, Butte Co., CA	CAS 205830; AF258939

Appendix *Continued*

Taxon	Sample no.	TreeMap locality	Haplotype no.	General locality, county, and state	Specimen no. GenBank no.
E. m. multicarinata	6		NC5	Jack Creek, Butte Co., CA	CAS 205836; AF258914
E. m. multicarinata	7	D	NC6	Nevada City, Nevada Co., CA	MVZ 175428; AF258915
E. m. multicarinata	8		′	Foresthill, Placer Co., CA	MVZ 175432; AF258915
E. m. multicarinata	9		NC7	Georgetown, El Dorado Co., CA	MVZ 150172; AF258916
E. m. multicarinata	10	E	NC8	Avery, Calaveras Co., CA	MVZ 162066; AF258917
E. m. multicarinata	11		NC9	West Point, Calaveras Co., CA	MVZ 175287; AF258918
E. m. multicarinata	12		NC10	Hwy 101 and 128 jct., Mendocino Co., CA	MVZ 162059; AF258919
E. m. multicarinata	13		NC11	Little Sullivan Creek, Colusa Co., CA	CAS 212751; DQ364660
E. m. multicarinata	14	N	NC12	Geyserville, Sonoma Co., CA	MVZ 162054; AF258920
E. m. webbi	15		NC13	Pine Flat Reservoir, Fresno Co., CA	CAS 208822; AF258933
E. m. webbi	16		NC14	Democrat Hot Spring, Kern Co., CA	MVZ 137822; AF258936
E. m. multicarinata	17		NC15	Gazos Creek, San Mateo Co., CA	CRF 170; AF258923
E. m. multicarinata	18	L	NC16	University Calif. Santa Cruz, Santa Cruz Co., CA	MVZ 227752; AF258924
E. m. webbi	19		SSN1	Elderwood, Tulare Co., CA	MVZ 137828; AF258934
E. m. webbi	20	F	SSN2	Glennville, Kern Co., CA	CAS 206440; AF258935
E. m. multicarinata	21	M	C1	Briones Reservoir, Contra Costa Co., CA	MVZ 162061; AF258921
E. m. multicarinata	22		C2	Corral Hollow, Alameda Co., CA	CRF 10; AF258922
E. m. multicarinata	23		′	Sunol, Alameda Co., CA	CAS 208964; AF258922
E. m. multicarinata	24		C3	Escondido Campground, Monterey Co., CA	CAS 208948; AF258925
E. m. multicarinata	25	K	′	Hastings University Calif. Reserve, Monterey Co., CA	CRF 144; AF258925
E. m. multicarinata	26		C4	Hastings University Calif. Reserve, Monterey Co., CA	CAS 205794; AF258926
E. m. multicarinata	27		C5	Hwy 146 and 25 jct., San Benito Co., CA	MVZ 227747; AF258927
E. m. multicarinata	28		C6	Mercy Hot Springs, Fresno Co., CA	MVZ 228811; AF258928
E. m. multicarinata	29	J	C7	Cuesta Ridge, San Luis Obispo Co., CA	MVZ 150173; AF258929
E. m. multicarinata	30		C8	Stoney Creek, San Luis Obispo Co., CA	CAS 208514; AF258930
E. m. multicarinata	31		′	Stoney Creek, San Luis Obispo Co., CA	CAS 208515; AF258930
E. m. multicarinata	32		C9	Buellton, Santa Barbara Co., CA	MVZ 137539; AF258931
E. m. multicarinata	33		C10	Goleta, Santa Barbara Co., CA	MVZ 162381; AF258932
E. m. webbi	34		SC1	Tehachapi Mountain Park, Kern Co., CA	CAS 214889; AF258937
E. m. webbi	35		SC2	W. of Frazier Park, Kern Co., CA	CAS 214887; AF258938
E. m. webbi	36		′	W. of Frazier Park, Kern Co., CA	CAS 214888; AF258938
E. m. webbi	37		SC3	W. of Independence, Inyo Co., CA	MVZ 227733; AF258940
E. m. webbi	38		′	S. of Olancha, Inyo Co., CA	MVZ 227739; AF258940
E. m. webbi	39		SC4	Lone Pine, Inyo Co., CA	CAS 206443; AF258941
E. m. webbi	40		′	Santa Catalina Island, Los Angeles Co., CA	SDSU 4071; AF258941
E. m. webbi	41		SC5	Los Angeles, Los Angeles Co., CA	LACM 145480; AF258942
E. m. webbi	42	G	SC6	Malibu Creek, Los Angeles Co., CA	CRF 146; AF258943
E. m. webbi	43		SC7	Lucerne Valley, San Bernardino Co., CA	MVZ 227748; AF258944
E. m. webbi	44	H	SC8	San Timoteo Canyon, Riverside Co., CA	CAS 208712; AF258945
E. m. webbi	45	I	SC9	Hwy 6 and 7 jct., San Diego Co., CA	MVZ 162058; AF258946
E. m. webbi	46		SC10	El Rosario, Baja Calif. Norte, Mexico	MVZ 161393; AF258947
E. m. nana	47		SC11	Coronados Island, Baja Calif. Norte, Mexico	GP 444; DQ364661
E. panamintina	48		SC12	Silver Creek Canyon, Inyo Co., CA	RM 10712; AF258948

Appendix *Continued*

Taxon	Sample no.	TreeMap locality	Haplotype no.	General locality, county, and state	Specimen no. GenBank no.
E. panamintina	49		SC13	N. of Big Pine, Inyo Co., CA	MVZ 227761; AF258949
E. panamintina	50		SC14	E. of Lone Pine, Inyo Co., CA	MVZ 227763; AF258950
E. panamintina	51		SC15	Grapevine Canyon, Inyo Co., CA	MVZ 191076; AF258951
E. paucicarinata	52			La Laguna, Baja Calif. Sur, Mexico	MVZ 191079; AF258954
E. paucicarinata	53			San Antonia de la Sierra, Baja Calif. Sur, Mexico	MVZ 236263; DQ364662
E. kingii	54			Hwy 152 and 61 jct., Grant Co., NM	UTACV 47131; AF258952
E. kingii	55			Bear Canyon, Pima Co., AZ	CAS 208956; AF258953
E. coerulea				Jackson State Forest, Mendocino Co., CA	CAS 206446; AF258955
E. coerulea				Leggett, Mendocino Co., CA	MVZ 162041; AF258956
Charina bottae complex					
C. bottae	1	K	NW1	Hwy 1, N. of Nacimiento Road, Monterey Co., CA	MVZ 229876; AF302945
C. bottae	2	L	NW2	Santa Cruz Mountains, Santa Cruz Co., CA	CAS 205801; AF302946
C. bottae	3		′	San Francisco Watershed, San Mateo Co., CA	CAS 204822; AF302947
C. bottae	4	M	NW3	University Calif. Berkeley, Alameda Co., CA	MVZ 164925; AF302948
C. bottae	5	N	NW4	Ida Clayton Road, near Hwy 128, Napa Co., CA	no voucher; AF302949
C. bottae	6		NW5	Eagle Lake, Lassen Co., CA	SJA 22800; AF302950
C. bottae	7	C	′	Rock Creek, Shasta Co., CA	CSPU 2222; AF302951
C. bottae	8		NW6	Cedar Canyon, Modoc Co., CA	MVZ 162364; AF302952
C. bottae	9		NW7	Corvallis, Benton Co., OR	CSPU 2224; AF302953
C. bottae	10		NW6	Corvallis, Benton Co., OR	CSPU 2226; AF302954
C. bottae	11		′	Hwy 26, W, of Grant Co. line, Wheeler Co., OR	MVZ 162365; AF302955
C. bottae	12		′	SW. of Pullman, Whitman Co., WA	MVZ 230472; AF302956
C. bottae	13		NW8	Logan Canyon, Cache Co., UT	MVZ 230471; AF302957
C. bottae	14	D	SN1	FSR 17, Tahoe National Forest, Nevada Co., CA	CAS 209774; AF302958
C. bottae	15		SN2	Greenhorn Creek, Plumas Co., CA	CAS 206040; AF302959
C. bottae	16		SN3	Sagehen University Calif. Reserve, Nevada Co., CA	MVZ 162366; AF302960
C. bottae	17		SN2	Golden Trout Crossing Campground, Butte Co., CA	CAS 205637; AF302961
C. bottae	18		′	Gold Run Creek, Yuba Co., CA	CAS 205988; AF302962
C. bottae	19		′	S. of FSR 690, Plumas National Forest, Yuba Co., CA	CAS 206320; AF302963
C. bottae	20		SN4	Strawberry Creek, El Dorado Co., CA	CSPU 2225; AF302964
C. bottae	21		SN5	Leavitt Meadows, Mono Co., CA	MVZ 150180; AF302965
C. bottae	22	E	SN6	Sourglass Crossing, Tuolomne Co., CA	MVZ 197551; AF302966
C. bottae	23		SN7	S. of Lake Cherry, Tuolomne Co., CA	MVZ 230470; AF302967
C. bottae	24		SN8	Yosemite National Park, Mariposa Co., CA	CSPU 2232; AF302968
C. bottae	25		′	North Fork Willow Creek, Madera Co., CA	CAS 209228; AF302969
C. bottae	26		SN9	unknown locality, Tulare Co., CA	CSPU 2223; AF302970
C. bottae	27		SN10	Piute Mountains, Kern Co., CA	no voucher; AF302971
C. bottae	28	F	SN11	Breckenridge Mountain, Kern Co., CA	MVZ 229991; AF302972
C. bottae	29		SN12	Breckenridge Mountain, Kern Co., CA	MVZ 229992; AF302973
C. bottae	30		SN13	McGill Campground, Kern Co., CA	CSPU 2231; AF302974
C. bottae	31		SN14	Tehachapi Mountains, Kern Co., CA	no voucher; AF302975
C. bottae	32		SN15	Camp Earl Anna, Kern Co., CA	CSPU 2228; AF302976

Appendix *Continued*

Taxon	Sample no.	TreeMap locality	Haplotype no.	General locality, county, and state	Specimen no. GenBank no.
C. umbratica	33		SC1	Green Valley Road, San Bernardino Co., CA	CSPU 2219; AF302977
C. umbratica	34		SC2	Twin Peaks, San Bernardino Co., CA	CSPU 2220; AF302978
C. umbratica	35		SC3	Heaps Peak Heliport, San Bernardino Co., CA	CSPU 2227; AF302979
C. umbratica	36		SC4	Baldwin Lake, San Bernardino Co., CA	no voucher; AF302980
C. umbratica	37	H	SC5	Fern Valley, Idyllwild, Riverside Co., CA	CSPU 2229; AF302981
C. umbratica	38		SC6	Humber Park, Idyllwild, Riverside Co., CA	CSPU 2230; AF302982
Lampropeltis zonata					
L. z. agalma	1		SC1	Laguna Hansen, Baja Calif. Norte, Mexico	no voucher; AF136189
L. z. agalma	2		SC2	Laguna Hansen, Baja Calif. Norte, Mexico	no voucher; AF136190
L. z. agalma	3		SC3	Sierra San Pedro Martir, Baja Calif. Norte, Mexico	no voucher; AF136191
L. z. herrerae	4		SC4	South Todos Santos Island, Baja Calif. Norte, Mexico	no voucher; AF136192
L. z. herrerae	5		’	South Todos Santos Island, Baja Calif. Norte, Mexico	no voucher; AF136192
L. z. multicincta	6		NC1	Kyburz, El Dorado Co., CA	MVZ 229879; AF136193
L. z. multicincta	7		NC2	Bass Lake, Madera Co., CA	no voucher; AF136194
L. z. multicincta	8	E	NC3	Greeley Hill, Mariposa Co., CA	no voucher; AF136195
L. z. multicincta	9		NC4	Hwy 70, near Quincy, Plumas Co., CA	no voucher; AF136196
L. z. multicincta	10	D	’	Hwy 49, near Downieville, Sierra Co., CA	MVZ 229910; AF136217
L. z. multicincta	11	F	C1	North fork of Middle Fork Tule River, Tulare Co., CA	no voucher; AF136197
L. z. multicincta	12		NC5	Pinecrest Lake, Tuolomne Co., CA	no voucher; AF136198
L. z. multifasciata	13		C2	Tehachapi Mountains, Kern Co., CA	MVZ 229881; AF136199
L. z. multifasciata	14	K	C3	Bottcher’s Gap, Monterey Co., CA	MVZ 229883; AF136200
L. z. multifasciata	15		C4	Santa Barbara, Santa Barbara Co., CA	RES mf40; AF136201
L. z. multifasciata	16	L	C5	Ben Lomond, Santa Cruz Co., CA	MVZ 229893; AF136202
L. z. multifasciata	17		C6	near Watsonville, Santa Cruz Co., CA	no voucher; AF136203
L. z. multifasciata	18		C7	near Frazier Park, Ventura Co., CA	RES mf41; AF136204
L. z. parvirubra	19		SC5	West Fork, Los Angeles Co., CA	no voucher; AF136205
L. z. parvirubra	20	H	SC6	Black Canyon, Riverside Co., CA	no voucher; AF136206
L. z. parvirubra	21		SC7	Running Springs, San Bernardino Co., CA	no voucher; AF136207
L. z. pulchra	22	G	SC8	Decker School Road, Los Angeles Co., CA	no voucher; AF136208
L. z. pulchra	23	I	SC9	Mount Laguna, San Diego Co., CA	MVZ 229888; AF136209
L. z. pulchra	24		SC10	Palomar Mountain, San Diego Co., CA	MVZ 229889; AF136210
L. z. pulchra	25		SC11	Santa Ana Mountains, Orange Co., CA	no voucher; AF136211
L. z. zonata	26	N	NC6	Western Mines Road, Lake Co., CA	MVZ 225913; AF138762
L. z. zonata	27		NC7	Hwy 175, near Hopland Grade, Mendocino Co., CA	MVZ 229882; AF136212
L. z. multicincta × *zonata*	28	C	NC8	Dunsmuir, Siskiyou Co., CA	MVZ 225915; AF136213
L. z. multicincta × *zonata*	29		NC9	Hwy 96, near Hamburg, Siskiyou Co., CA	MVZ 225917; AF136214
L. z. multicincta × *zonata*	30	O	NC4	Rattlesnake Creek, Forest Glen, Trinity Co., CA	no voucher; AF136215
L. z. multicincta × *zonata*	31	B	NC10	NE of Ashland, Jackson Co., OR	MVZ 225920; AF136216
L. z. multicincta × *zonata*	32		NC4	near Bingen, Klickitat Co., WA	MVZ 229908; AF136217
L. z. zonata × *multifasciata*	33		NC11	Mount Hamilton, Santa Clara Co., CA	no voucher; AF136218
L. z. zonata × *multifasciata*	34		C8	S. of Mount Hamilton, Santa Clara Co., CA	MVZ 229891; AF136219

