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ORIGINAL ARTICLE

Closing the ring: historical biogeography of the salamander ring species *Ensatina eschscholtzii*

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ABSTRACT

Aim The salamander *Ensatina eschscholtzii* Gray is a classic example of a ring species, or a species that has expanded around a central barrier to form a secondary contact characterized by species-level divergence. In the original formulation of the ring species scenario, an explicit biogeographical model was proposed to account for the occurrence of intraspecific sympatry between two subspecies in southern California (the 'southern closure' model). Here we develop an alternative ring species model that is informed by the geomorphological development of the California Coast Ranges, and which situates the point of ring closure in the Monterey Bay region of central coastal California (the 'Monterey closure' model). Our study has two aims. The first is to use phylogenetic methods to evaluate the two competing biogeographical models. The second is to describe patterns of phylogeographical diversity throughout the range of the *Ensatina* complex, and to compare these patterns with previously published molecular systematic data.

Location Western North America, with a focus on the state of California, USA.

Methods We obtained mitochondrial DNA sequence data from 385 individuals from 224 populations. A phylogeny was inferred using Bayesian techniques, and the geographical distributions of haplotypes and clades were mapped. The two biogeographical ring species models were tested against our Bayesian topology, including the associated Bayesian 95% credible set of trees.

Results High levels of phylogeographical diversity were revealed, especially in central coastal and northern California. Our Bayesian topology contradicts the Monterey closure model; however, 0.08% of the trees in our Bayesian 95% credible set are consistent with this model. In contrast, the classic ring species biogeographical model (the southern closure model) is consistent with our Bayesian topology, as were 99.92% of the trees in our 95% credible set.

Main conclusions Our Bayesian phylogenetic analysis most strongly supports the classic ring species model, modified to accommodate an improved understanding of the complex geomorphological evolution of the California Coast Ranges. In addition, high levels of phylogeographical diversity in central and northern California were identified, which is consistent with the striking levels of allozymic differentiation reported previously from those regions.

Keywords

Bayesian analysis, biogeography, California, geomorphology, mitochondrial DNA, phylogeography, speciation, species concepts.

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INTRODUCTION

Ring species exhibit a circular arrangement of populations around a central barrier, with reproductively isolated parts overlapping at one point in the ring, yet with morphological and genetic intergradation elsewhere (Mayr, 1942, 1963). They arise when two or more lineages descend from a common ancestor and become reproductively isolated while maintaining their genetic connectivity through a chain of interbreeding populations. Mayr (1963, p. 507) stated that ring species are 'the perfect demonstration of speciation' because they illustrate how the microevolutionary processes generating intraspecific geographical variation can lead to species-level divergence. When geographical variation in characters has an adaptive basis, ring species present a natural example of how adaptive diversification interacts with geography to promote species formation (Mayr, 1942, 1963; Irwin *et al.*, 2001; Wake, 2006; Martens & Päckert, 2007). The intraspecific sympatry found in ring species also leads to serious taxonomic difficulties, drawing attention to the shortcomings of traditional Linnaean taxonomy and bringing the species problem into sharper focus (e.g. Highton, 1998; Wake & Schneider, 1998; Wake, 2006).

The salamander *Ensatina eschscholtzii* Gray, 1850 is a particularly influential example of a ring species (Ridley, 1996; Futuyma, 1998). Stebbins (1949) recognized seven subspecies in the complex, including four with a relatively uniform dorsal coloration (the 'unblotched' subspecies *picta*, *oregonensis*, *xanthoptica*, *eschscholtzii*) and three with bright dorsal patches of colour overlaid on a dark background (the 'blotched' subspecies *platensis*, *croceater*, *klauberi*) (for drawings and photographs see Stebbins, 2003; Wake, 2006). Together these subspecies are distributed in a ring around the Central Valley of California, which is hot and arid and currently presents an environment that is inhospitable to terrestrial salamanders (Fig. 1a). However, in the mountains of southern California, the unblotched subspecies *eschscholtzii* and the blotched subspecies *klauberi* are locally sympatric with either limited or no hybridization, indicating they have reached the species level of divergence (Fig. 1a; Stebbins, 1949, 1957; Brown, 1974; Wake *et al.*, 1986). Stebbins (1949) developed an explicit biogeographical model to account for this taxonomic oddity of sympatric subspecies. He postulated that the *Ensatina* complex originated in present-day northern California and southern Oregon, perhaps from a *picta*-like ancestor. This ancestral stock then expanded its distribution as two arms southward down the Coast Ranges (unblotched subspecies) and the inland ranges (blotched subspecies), the arms adapting and diverging as they spread, until they re-established contact in southern California as reproductively isolated entities (Fig. 1a). Broad zones of phenotypic intergradation between adjacent subspecies were interpreted as representative of ongoing genetic connectivity (Dobzhansky, 1958), and the two sympatric subspecies in southern California were thereby viewed as linked together by a continuous sequence of interbreeding populations, thus forming a ring species.

Much molecular systematic work has been done on the *Ensatina* complex since Stebbins (1949). The results are complex in detail, but support the major tenets of the ring species hypothesis in finding that secondary contacts between the coastal and inland arms are characterized by species-level divergence, while secondary contacts within the arms exhibit patterns of intergradation and genetic merger (Wake & Yanev, 1986; Wake *et al.*, 1986, 1989; Moritz *et al.*, 1992; Jackman & Wake, 1994; Wake, 1997; Alexandrino *et al.*, 2005). The only study to present a phylogenetic hypothesis for the *Ensatina* complex, however, was that of Moritz *et al.* (1992), which used 24 mitochondrial (mtDNA) cytochrome *b* sequences sampled throughout the range of the species. Their results supported the ring species scenario in that independent coastal (*xanthoptica*, *eschscholtzii*) and inland (southern *platensis*, *croceater*, *klauberi*) clades were identified. In their best-estimate phylogeny, these two clades were recovered as sister taxa, with northern lineages of *oregonensis* and *platensis* occupying basal positions (Fig. 1b).

A detailed follow-up study to Moritz *et al.*'s (1992) is needed because the substantial phylogeographical structure within the *Ensatina* complex remains poorly demarcated, and because allozyme studies have uncovered a multifaceted biogeographical history, the hierarchical organization of which remains unclear (Wake & Yanev, 1986; Jackman & Wake, 1994; Wake, 1997). In addition, following the publication of Moritz *et al.* (1992), Parks (2000) estimated a Miocene origin for the *Ensatina* complex. The geomorphology of western North America differed dramatically in the Miocene from that of today (Yanev, 1980; Hall, 2002), and a full understanding of the ring species biogeography for *Ensatina* must incorporate knowledge of the geomorphological evolution of the region (e.g. Wake, 1997).

Here we present a new phylogeny for the *Ensatina* complex generated using mitochondrial DNA sequences. The current study expands on that of Moritz *et al.* (1992) by including 385 sequences from 224 populations. One aim of the study is to introduce a novel biogeographical model based strictly on the geomorphological evolution of the California Coast Ranges, developed as an alternative to the classic ring species model of Stebbins (1949). Our second aim is to provide a description of patterns of phylogenetic and phylogeographical diversity, including mapping the distribution of mtDNA haplotype lineages in California. These results are used to distinguish between the two competing biogeographical models.

The biogeography of ring closure

The Coast Ranges of California are composed of northern and southern elements that have only recently been made continuous (Fig. 2). Orogeny of the northern Coast Ranges was the result of uplift caused by interactions between the Pacific and North American plates (Atwater, 1970). In contrast, assorted elements of the central and southern Coast Ranges were initially part of a land mass known as the Salinian terrain. Thirty million years ago, during Oligocene times, the Salinian terrain was located off the coast of present-day southern

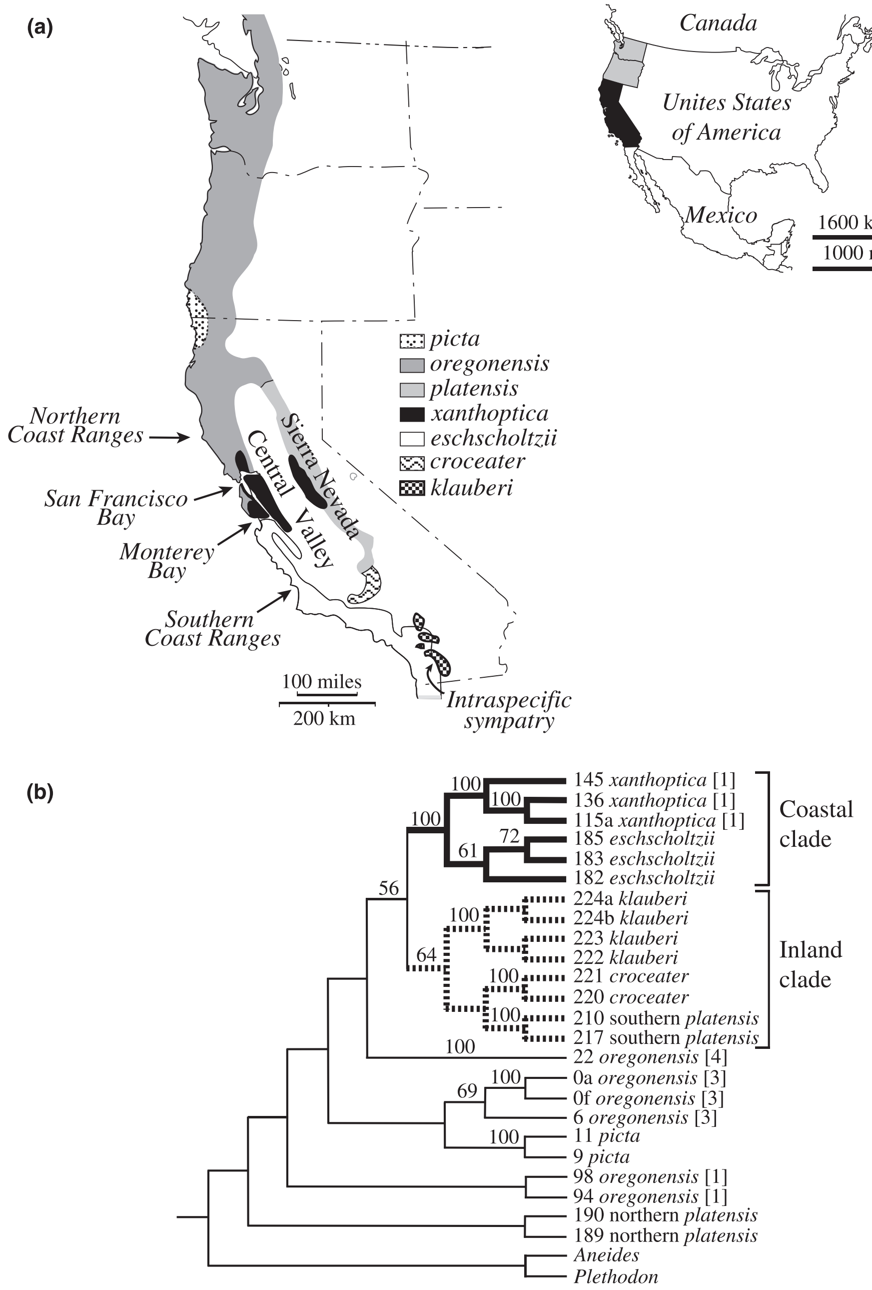


Figure 1 (a) Map showing the distribution of subspecies of *Ensatina eschscholtzii* in western North America. In the USA, the state of California is highlighted in black; Washington and Oregon are shown in grey. Subspecies, which circumscribe patterns of phenotypic variation (Stebbins, 1949), are differentially shaded. In southern California, the subspecies *eschscholtzii* and *klauberi* are locally sympatric in places with limited or no interbreeding. Note the locations of San Francisco Bay and Monterey Bay. (b) Best-estimate phylogeny from Moritz *et al.* (1992), showing the recovered relationships among 24 mtDNA cytochrome *b* sequences, plus two outgroup taxa. Individual samples are relabelled to correspond with the names and population numbering scheme used in this paper. This tree was constructed using parsimony analysis (see Moritz *et al.*, 1992, for details); numbers above branches indicate bootstrap support (100 replicates) for values > 50%.

California (Hall, 2002). Thereafter, from the mid-Miocene (*c.* 18 Ma) onward, fragments of this land mass formed islands that slid northward and were incorporated into the Coast Ranges of central coastal California (Hall, 2002; Wake, 2006). Nonetheless, as recently as 2 Ma the Coast Ranges remained divided by the outlet of a large marine embayment that extended into the Central Valley of California through the present-day Monterey Bay region (Yanev, 1980; Hall, 2002) (Fig. 2b). This barrier was altered when continuing uplift closed off the marine embayment, transforming the southern

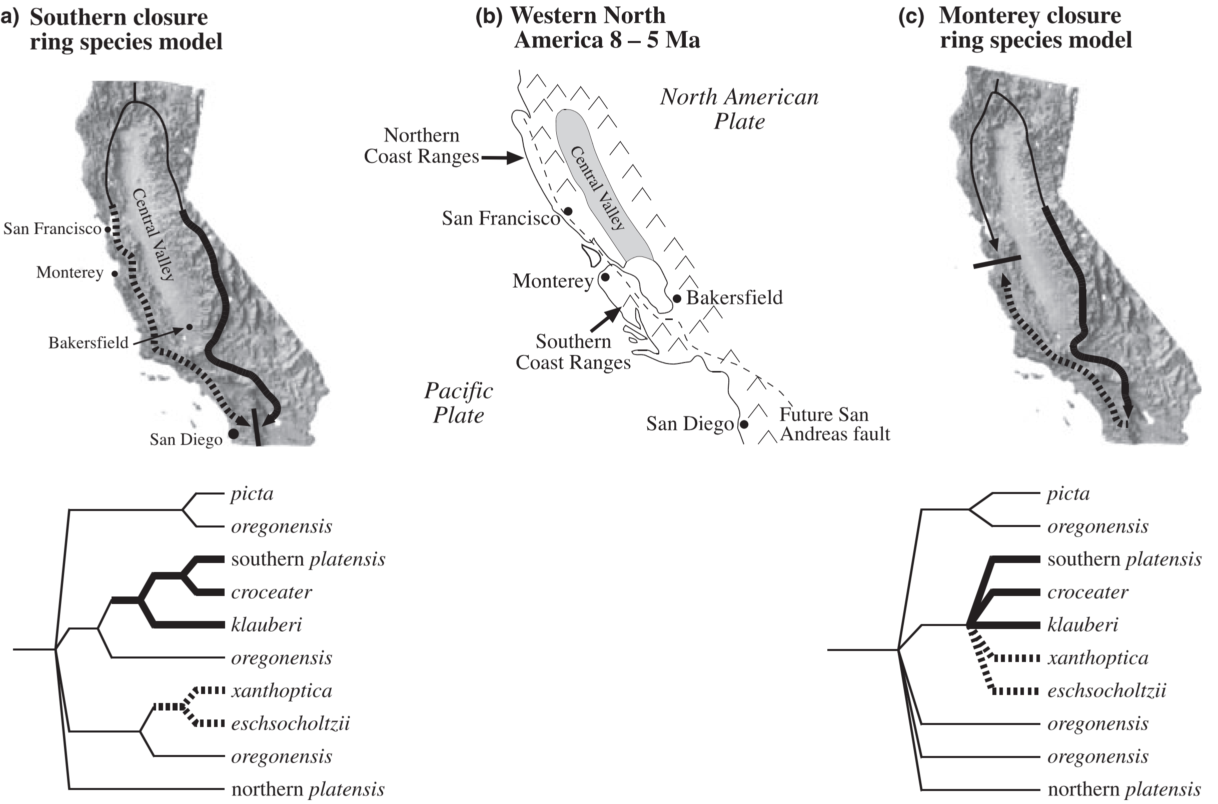


Figure 2 Biogeographical models and corresponding phylogenetic hypotheses. (a) Stebbins's (1949) southern closure ring species hypothesis. This model is supported if the recovered phylogeny identifies independent coastal (*xanthoptica*, *eschscholtzii*) and inland (southern *platensis*, *croceater*, *klauberi*) clades, with northern lineages (*oregonensis* and *picta*) basal. (b) The coast of California 8–5 Ma, when the present day Coast Ranges were divided into northern and southern halves by a marine embayment (Hall, 2002). (c) The Monterey closure ring species hypothesis. This model is supported if the coastal and inland clades are most closely related, with northern lineages basal. In both (a) and (c), the phylogenetic models account for what is already understood about the phylogeny of the *Ensatina* complex: that *oregonensis* is a deeply diverged, paraphyletic assemblage of lineages, that *picta* is nested within *oregonensis*, and that *platensis* is composed of two unrelated mtDNA clades (Moritz *et al.*, 1992).

Central Valley into an enormous freshwater lake (Dupré, 1990; Sims, 1993). Like the marine embayment, this lake drained into Monterey Bay via the wide Salinas and Pajaro River valleys (Sarna-Wojcicki *et al.*, 1985), and the Monterey Bay region probably remained a dispersal barrier for many terrestrial organisms. Finally, 600,000 years ago the drainage of the Central Valley shifted northward to exit just north of present-day San Francisco (Fig. 2a), eliminating the geographical barrier at Monterey Bay (Sarna-Wojcicki *et al.*, 1985).

The Monterey Bay region thus constitutes a historical barrier, and today many taxa show concordant phylogeographical breaks there (Calsbeek *et al.*, 2003; Lapointe & Rissler, 2005; Feldman & Spicer, 2006; Kuchta & Tan, 2006; Rissler *et al.*, 2006). Because the origins of the coastal and inland arms of the *Ensatina* complex are thought to pre-date the formation of a continuous California Coast Range system (Wake, 1997), the Monterey Bay region should represent a fundamental biogeographical barrier for *Ensatina* as well. Recognizing this, Wake (1997) proposed that the ancestors of the coastal clade (*xanthoptica*, *eschscholtzii*) dispersed out to a piece of the Salinian terrain prior to its merger with the North American plate. Later, after the Coast Ranges became contiguous, *eschscholtzii* would have expanded southward to form a secondary contact with *klauberi* in present-day southern California. This scenario is consistent with the geomorphological evolution of the California Coast Ranges, and is also consistent with the classic ring species interpretation of the *Ensatina* complex because the coastal and inland arms evolved in the north and dispersed southward to form a secondary contact in southern California. From a phylogenetic perspective, the ring species hypothesis of Stebbins (1949) predicts that the coastal clade (*xanthoptica*, *eschscholtzii*) and the inland clade (southern *platensis*, *croceater*, *klauberi*) are each derived independently from a northern ancestor (Fig. 2a). We call this scenario the southern closure model because it situates the point of ring closure in southern California.

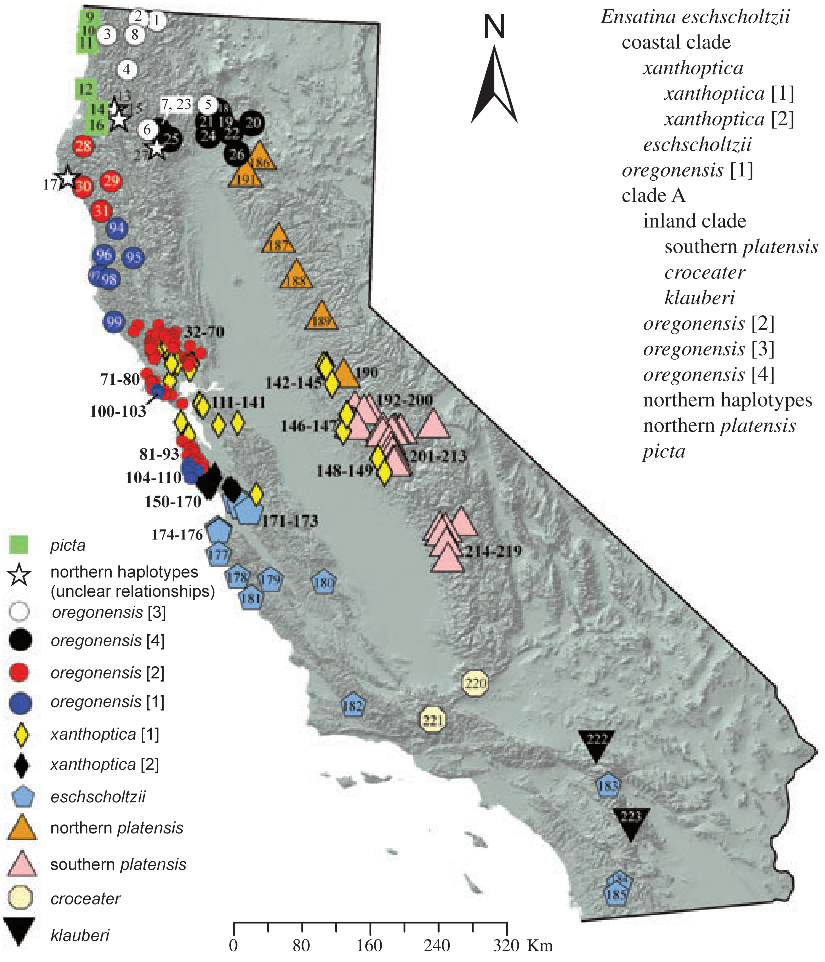
An alternative biogeographical hypothesis, based on the geological formation of the California Coast Ranges, is that the Monterey Bay region, rather than the mountains of southern California, is the ultimate point of ring closure in the *Ensatina* complex. Under this scenario, *Ensatina* originated in northern California and expanded southward, yet was prevented from dispersing the length of the California coastline by the Monterey embayment (Fig. 2c). The inland clade (the ancestors of southern *platensis*, *croceater* and *klauberi*), on the other hand, was free to expand into southern California, where it gave rise to the coastal clade (*xanthoptica*, *eschscholtzii*). Ancestors of the coastal clade (which either lost their dorsal blotching or pre-dated the origin of the blotched phenotype) then expanded northward to the southern limit of the Monterey embayment. When the drainage of the Central Valley shifted to the Golden Gate north of San Francisco, the ring of populations closed. We call this new ring species scenario the Monterey closure model. The key phylogenetic prediction of the Monterey closure model is that the coastal and inland clades are closely related, with lineages in northern California ancestral to them (Fig. 2c). Indeed, this is exactly the pattern of relationships recovered by the best-estimate phylogeny of Moritz *et al.* (1992), although it was weakly supported (bootstrap = 56%; Fig. 1b).

MATERIALS AND METHODS

Population sampling and laboratory techniques

Populations are defined here as samples within 1 km of each other that belong to the same mtDNA haplotype lineage. For this study, a fragment of the cytochrome *b* (cyt *b*) gene was obtained from 224 populations (385 individuals) throughout the range of *E. eschscholtzii*, including 23 populations (24 individuals) sampled by Moritz *et al.* (1992) (see Appendix S1 in Supporting Information; Fig. 1b). The complete data set includes overlapping mtDNA haplotypes collected using two different sequencing technologies. For 39 haplotypes, the primers MVZ15 and Cytb2 were used to amplify the region between nucleotide positions 19–405 of the mtDNA cyt *b* locus (Moritz *et al.*, 1992). Sequences were obtained by running labelled single-strand polymerase chain reaction (PCR) products on acrylamide gels (manual sequencing; see Moritz *et al.*, 1992 for laboratory details). The average length of these sequences was 439 bp (range 242–625).

For the remaining 322 haplotypes, whole genomic DNA was extracted from ethanol-preserved or frozen tissues (tail tips, liver, heart) using the Qiagen DNeasy Tissue Kit (Qiagen, Valencia, CA, USA). The primers MVZ15 and MVZ16 (Moritz *et al.*, 1992) were used to amplify the region of the mtDNA *cyt b* gene between nucleotide positions 19 and 804. Amplifications were carried out in a PTC-100 Thermal Cycler (M.J. Research, Waltham, MA, USA) as follows: 94°C for 1.5 min (initial denaturation); 35 cycles at 94°C for 1 min, 49°C for 1 min, and 72°C for 1 min.



Ensatina eschscholtzii
- coastal clade
  - *xanthoptica*
    - *xanthoptica* [1]
    - *xanthoptica* [2]
  - *eschscholtzii*
- *oregonensis* [1]
- clade A
  - inland clade
    - southern *platensis*
    - *croceater*
    - *klauberi*
  - *oregonensis* [2]
  - *oregonensis* [3]
  - *oregonensis* [4]
  - northern haplotypes
  - northern *platensis*
  - *picta*

Figure 3 Map showing the distribution of samples of *Ensatina eschscholtzii* in California. Samples assigned to the same subspecies are given the same symbol, and colours are used to separate clades within subspecies. Nine populations north of California are not shown. Population numbers correspond to those in Appendix S1, and are used throughout the manuscript. The table (upper right) provides a reference for the names used here, with the pattern of indentation corresponding to nested clades (Fig. 4a).

Amplification reaction mixtures consisted of 1× PCR buffer with 1.5 mM $MgCl_2$, 40 mM of each dNTP, 10 μM of each primer, and 0.75 U *Taq* DNA polymerase in a total volume of 25 μL. PCR experiments included non-template controls to monitor contamination. Double-stranded PCR products were purified using the QIAquick PCR Purification kit (Qiagen). All samples were sequenced in both directions in a 10-μL reaction mixture using dRhodamine and a 377 Automated Sequencer (Applied Biosystems, Foster City, CA, USA). Sequences were visually aligned in SEQUENCHER (Gene Codes, Ann Arbor, MI, USA). The average sequence length was 664 bp (range: 331–784). All GenBank accession numbers are listed in Appendix S1.

Phylogenetic analysis

Partitioned Bayesian phylogenetic analyses were carried out using MRBAYES ver. 3.04b (Huelsenbeck & Ronquist, 2001). The data set was divided into three partitions: 1st, 2nd and 3rd codon positions. For each partition the best-fitting model of nucleotide substitution was selected using the Akaike information criterion as implemented in MRMODELTEST ver. 1.1b (Nylander, 2004). The models selected were: HKY + Γ, HKY + I + Γ, and GTR + Γ for the 1st, 2nd and 3rd codon positions, respectively. Flat Dirichlet prior distributions were used for substitution rates and base frequencies, and default flat prior distributions were used for all other parameters. Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were run with one cold and three heated chains (temperature set to the default value of 0.2) for 20 million generations and sampled every 1000 generations. Stationarity was confirmed by examining plots of $-\ln L$ scores and parameter values. The phylogeny was rooted with 10 outgroups from Mueller *et al.* (2004): *Plethodon cinereus*, *P. petraeus*, *P. elongatus*, *Desmognathus wrighti*, *D. fuscus*, *Phaeognathus hubrichti*, *Hydromantes brunus*, *Speleomantes italicus*, *Aneides hardii* and *A. flavipunctatus* (GenBank accession numbers NC006343–NC006345, NC006334, NC006335, NC006337–NC006339, AY728215, NC006327). Two additional outgroup sequences from Moritz *et al.* (1992) were also included: *Aneides lugubris* (L75820) and *Plethodon elongatus* (L75821). The sister taxon of *Ensatina* is currently unclear, but these outgroups include representatives of all the genera that have been inferred to be most closely related to *Ensatina* (Chippindale *et al.*, 2004; Mueller *et al.*, 2004; Vieites *et al.*, 2007). In addition, the inclusion of multiple outgroups was necessary for calibrating our divergence time estimates (described below).

Twelve haplotypes in our complete data set were excluded from the Bayesian phylogenetic analysis because they were very short, or were of low quality (Appendix S1). These were later assigned to clades using a neighbour-joining analysis with maximum likelihood distances, and in all cases the haplotypes were assigned to a geographically logical clade with high confidence (> 95% bootstrap support; data not shown). Individuals from these localities are plotted in Fig. 3 because they help to identify the geographical bounds of haplotype lineages.

Divergence time estimates

Using a simple molecular clock, Parks (2000) estimated that the coastal clade (*xanthoptica*, *eschscholtzii*) of the *Ensatina* complex originated at least 10 Ma. If this is correct, the coastal clade pre-dates the development of a continuous Coast Range system in central coastal California (which formed 2–0.6 Ma; see Introduction), and thus could not have evolved *in situ* as postulated by Stebbins (1949). We estimated the age of the coastal clade using a Bayesian approach that does not assume constant evolutionary rates, as implemented in the software package 'multidistribute' (Thorne *et al.*, 1998; Thorne & Kishino, 2002). The fossil record for plethodontid salamanders is meagre, and no *Ensatina* fossils have been found (Holman, 2006). However, two fossils were useful for constraining divergence dates among outgroup taxa: the common ancestor of *H. brunus* and *S. italicus* was constrained to be at least 13.75 Myr old (Venczel & Sanchíz, 2005), and the common ancestor of *A. hardii* and *A. flavipunctatus* was constrained to be at least 23 Myr old (Tihen & Wake, 1981).

Comparing biogeographical models

Our two biogeographical models are the southern closure model (Stebbins, 1949; Fig. 2a) and the Monterey closure model (Fig. 2c). In evaluating these hypotheses, we take into account the composite nature of the subspecies *platensis*, and the fact that *picta* was postulated previously to be nested within a deeply diverged, multiply paraphyletic *oregonensis* (Moritz *et al.*, 1992; Jackman & Wake, 1994). The two competing biogeographical models (Fig. 2a,c) were compared with our Bayesian topology and with the topologies present in the Bayesian 95% credible set using MESQUITE ver. 1.1 (Maddison & Maddison, 2006). The 95% credible set of trees includes all the topologies that are statistically indistinguishable from the recovered Bayesian topology. Consequently, topologies not present in the 95% credible set are statistically rejected, while topologies within the credible set are not rejected (Huelsenbeck & Rannala, 2004).

RESULTS

Phylogenetic relationships

Plots of $-\ln L$ scores and other parameter values suggested that stationarity was achieved in the Bayesian phylogenetic analysis. To be conservative, the first five million generations were discarded as burn-in, leaving 15 million generations and 15,000 topologies in the data set. Branch lengths for a consensus phylogram were calculated from the means of the posterior probabilities, and the posterior probabilities of clades were calculated as the fraction of instances that each clade was recovered. Three major, basal clades are recovered in the

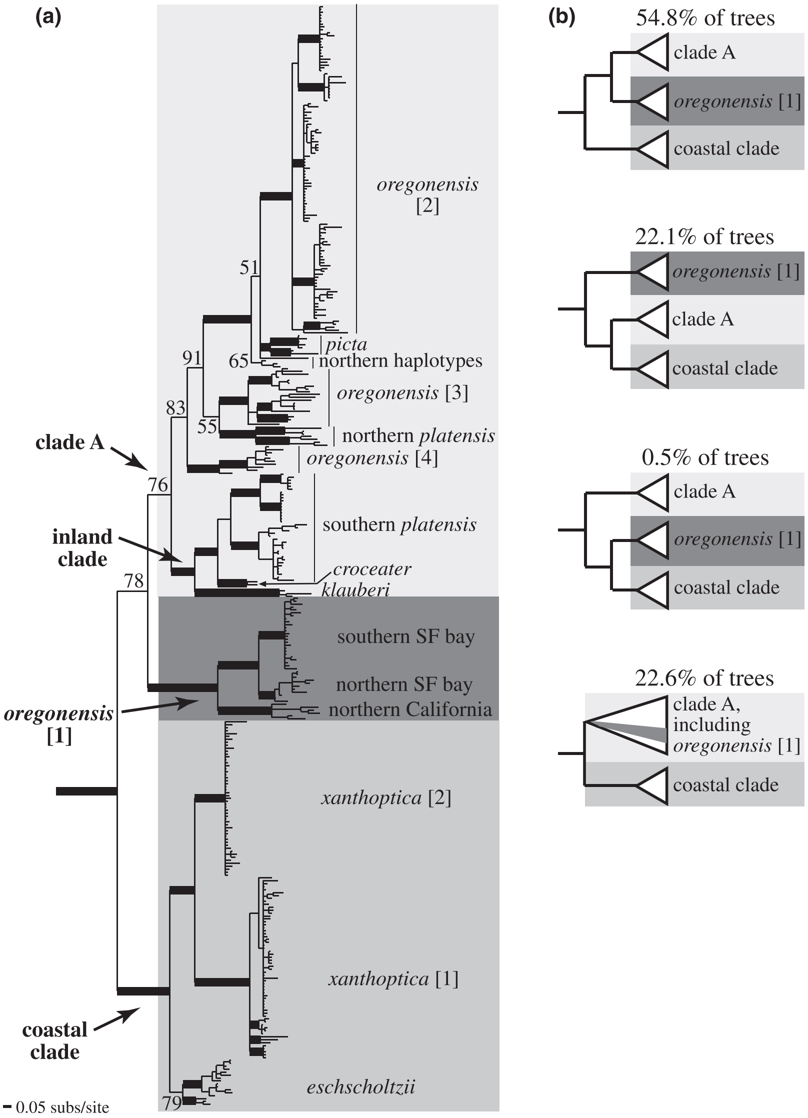


Figure 4 (a) Bayesian phylogenetic hypothesis for *Ensatina eschscholtzii*. Subspecies and the names of clades used in this paper are labelled to the right. Thick branches have posterior probabilities ≥ 95%. Branches of interest with posterior probabilities < 95% are labelled above the branch. Note that branches labelled 'northern haplotypes' have poor phylogenetic support and are not assigned to any particular haplotype lineage. (b) Basal branching patterns recovered in the Bayesian 95% credible set, illustrating the four possible phylogenetic placements of *oregonensis* [1]. The shading scheme matches (a). In the last reconstruction, which shows a lack of resolution at the base of the tree, eight trees (0.08% of the total) recover the coastal clade and the inland clade as sister taxa. The remaining 99.92% of the trees in the 95% credible set do not recover them as sister taxa.

Bayesian phylogeny, each of which contains substantial substructure (Fig. 4a). We refer to the clade including the subspecies *xanthoptica* and *eschscholtzii* as the coastal clade; a second clade, currently assigned to the subspecies *oregonensis*, is referred to as *oregonensis* [1]; and the third clade, including the rest of the *Ensatina* complex, we call clade A.

Coastal clade

The coastal clade includes the subspecies *xanthoptica* and *eschscholtzii*, and is strongly supported with a posterior probability (hereafter, PP) ≥ 95% (Fig. 4a). The subspecies *xanthoptica* (PP ≥ 95%) includes two haplotype lineages (both PP ≥ 95%), one of which is limited to the southern San Francisco peninsula (*xanthoptica* [1]; Figs 3 & 4a), and the other of which is found east and north of the San Francisco Bay region, as well as in the foothills of the Sierra Nevada (*xanthoptica* [2]; Figs 3 & 4a). The subspecies *eschscholtzii* also forms a monophyletic group, although, surprisingly, statistical support is weak (PP = 79%; Fig. 4a). Two well supported lineages (PP ≥ 95%) are recovered within *eschscholtzii*, however. One is found in southern California, and the other is located in central coastal California as far northward as the Pajaro river in the Monterey Bay area (Fig. 3).

oregonensis [1]

This clade is distributed along the coast of the northern half of California (Fig. 3). Within *oregonensis* [1] we recover three strongly supported lineages (Fig. 4a; PP ≥ 95%) with allopatric distributions: (1) along the coast of the southern San Francisco Peninsula; (2) a small patch of populations restricted to the Point Reyes peninsula, north west of San Francisco Bay; and (3) along the coast from northern Sonoma County northward to central Mendocino County in northern California (Fig. 3).

Clade A: northern lineages belonging to the subspecies oregonensis *and* picta

The third major clade recovered in the Bayesian analysis is clade A. This clade is not strongly supported (PP = 76%), but we recognize it here for communication purposes (see Comparing Biogeographical Models below). Multiple lineages possessing the unblotched *oregonensis* phenotype are members of clade A. One of these we call *oregonensis* [2] (Fig. 4a). Five geographically demarcated haplotype lineages are found within *oregonensis* [2], four of which are restricted to the San Francisco Bay region (Fig. 4a). A second clade, *oregonensis* [3] (Figs 3 & 4a), is distributed from northern California northward to central Washington State. It is most likely that this clade extends to the northern limit of the distribution of *Ensatina* in central coastal British Columbia, Canada. The final clade is *oregonensis* [4] (Fig. 4a), and it occupies a central position in the ring at the northern end of the Central Valley, where it forms a secondary contact with the northern clade of *platensis* (Fig. 3; Jackman & Wake, 1994; Wake & Schneider, 1998).

The northwestern-most clade in California, representing *picta*, is complex (Figs 3 & 4). Populations 9–12 form a lineage (PP ≥ 95%) within the traditional range of *picta*. Populations 14 and 16 to the south are sister to populations 9–12 (PP ≥ 95%), and are located within the range of Stebbins's (1949) *picta*/*oregonensis* intergrade zone. In contrast, population 3, located 11 km south east of *picta* population 10, is positioned within the eastern range limit of *picta* (Stebbins, 1949) yet belongs to the *oregonensis* [3] clade (Fig. 3).

Finally, not all the sequences from northern California are of clear phylogenetic affinity. We label these the 'northern haplotypes' (Fig. 4). One haplotype from Trinity County (population 27) is recovered as closely related to *picta* and *oregonensis* [2] (Fig. 4a). Three other haplotypes in north coastal California (populations 13, 15, 17) form a weakly supported clade (PP = 65%; Fig. 4a). These three populations are geographically close to population 27, *oregonensis* [2], *oregonensis* [3] and *picta* (Fig. 3).

Clade A: clades within the inland arm of the Ensatina *complex*

The inland clades (including northern *platensis*, as well as southern *platensis* + *croceater* + *klauberi*) possess blotched phenotypes and are distributed from the northern Sierra Nevada mountains southward to southern California (Fig. 1a). Haplotypes from the subspecies *platensis* form two unrelated clades corresponding to the northern and southern portions of the distribution of the subspecies; we call these two clades northern *platensis* and southern *platensis* (Figs 3 & 4a). In our analysis, northern *platensis* is strongly supported (PP ≥ 95%). Southern *platensis* is weakly supported (PP = 68%), but it is composed of two strongly supported subclades (PP ≥ 95%; Fig. 4a). Northern and southern *platensis* meet between populations 190 and 192 in the central Sierra Nevada (Fig. 3), *c.* 75 km north of a transition zone in allozymes (Jackman & Wake, 1994; Wake & Schneider, 1998).

The final two lineages in clade A represent the subspecies *croceater* and *klauberi*. The *croceater* lineage (PP ≥ 95%) is recovered as sister to southern *platensis* (PP ≥ 95%), with *klauberi* (PP ≥ 95%) sister to this clade (PP ≥ 95%; Fig. 4a). Together, these three lineages form a strongly supported inland clade (Fig. 4a). The relationship of this clade to the coastal clade (*xanthoptica*, *eschscholtzii*) is key to distinguishing between our two competing biogeographical models (Fig. 2a,c; see below).

Divergence time estimate

We estimated the age of the split between the coastal clade and clade A + *oregonensis* [1] at 21.5 Ma (95% CI = 8.9–51.1 Ma). A wide confidence interval was obtained because we were unable to constrain any of the nodes within the *Ensatina* complex with fossil calibrations, limiting our fossil dates to outgroup taxa. In addition, we were unable to put an upper bound on any node in the phylogeny, which is responsible for the large upper bound on the CI. Consequently, our estimate of the age of the coastal clade should be viewed with a high level of caution. Nonetheless, the lower estimate of 8.9 Myr for the origin of the coastal clade is in accordance with the simple molecular clock estimates of Parks (2000), and greatly precedes the formation of a continuous Coast Range system in central California, which formed no sooner than 2 Ma (Fig. 2b).

Comparing biogeographical models

We recovered separate, strongly supported coastal (*xanthoptica*, *eschscholtzii*) and inland (southern *platensis*, *croceater*, *klauberi*) clades in our phylogeny. The basal pattern of branching in our phylogeny has low statistical support (PP < 95%), however, which complicates the comparison of biogeographical models. Reference to the 95% credible set of trees provides insight into the statistically equivalent set of topologies; any topology present in this credibility set cannot be statistically rejected (Huelsenbeck & Rannala, 2004). There were 9500 trees in the Bayesian 95% credible set, and all identify separate coastal and inland clades (Fig. 4b). In 99.92% of these trees, the coastal and inland clades are not sister taxa, and thus they support the southern closure model (Fig. 2c). In eight of the topologies (0.08%), however, the inland and coastal clades are sister taxa, which is consistent with the southern closure model. Thus, while the Monterey closure model does not receive strong support, we are unable to reject it with statistical confidence.

The southern closure model (Stebbins, 1949) is more complex. Our Bayesian topology recovers the coastal clade (*xanthoptica*, *eschscholtzii*) as sister to the remainder of the *Ensatina* complex. This is consistent with the southern closure model (Stebbins, 1949) because it allows for the independent evolution of separate coastal and inland clades from a northern ancestor (Fig. 2a). Inspection of the Bayesian 95% credible set of trees revealed four sets of statistically indistinguishable topologies that differed in their branching patterns at the base of the tree, all four the result of an unstable placement of the *oregonensis* [1] clade (Fig. 4b). This clade is recovered as: (1) sister to clade A, as in our majority rule Bayesian topology (Fig. 4a); (2) sister to the coastal clade (*xanthoptica*, *eschscholtzii*); (3) sister to the rest of the *Ensatina* complex; or (4) nested within clade A (Fig. 4b). This latter reconstruction explains why clade A has low statistical support, despite the fact that no members of clade A are ever recovered outside that clade in the 95% credible set of trees. The strongest support for the southern closure hypothesis is provided by those topologies in which lineages of *oregonensis* are recovered as basal to both the coastal clade and the inland clade (sets 2 and 3 above; Fig. 4b).

DISCUSSION

Assembling a ring species

The phylogeographical complexity within *Ensatina* revealed by our study is likely to be a consequence of the old age of the complex (Maxson *et al.*, 1979; Larson *et al.*, 1981; Parks, 2000), combined with a vast geographical range relative to dispersal ability (Staub *et al.*, 1995) and the geomorphological complexities of the tectonically active California landscape (Yanev, 1980; Hall, 2002; Burnham, 2005). This set of circumstances has influenced patterns of diversification in diverse taxa (Kuchta & Tan, 2005; Feldman & Spicer, 2006; Chatzimanolis & Caterino, 2007; Rich *et al.*, 2008), including adaptive differentiation accompanying lineage divergence within the *Ensatina* complex itself (Kuchta, 2005; Wake, 2006; Kuchta *et al.*, 2008). Using a Bayesian approach, we estimated that the coastal clade (*xanthoptica*, *eschscholtzii*) originated prior to the formation of a continuous California Coast Range system, which closed between 2 Ma and 600,000 yr ago. Consequently, a strict interpretation of the southern closure ring species model (Fig. 2a) is problematic, because Stebbins (1949) explicitly predicted that the coastal arm of the *Ensatina* complex evolved within the present-day Coast Ranges. One solution that is consistent with the southern closure model was presented by Wake (1997), who postulated that the ancestor of the coastal clade colonized an island mass that was a geological precursor to part of the central Coast Ranges of California. An alternative solution, developed in this paper (Fig. 2c), postulates that ring closure in the *Ensatina* complex is located in the Monterey Bay region rather than southern California, and formed after uplift of the Coast Ranges created a continuous Coast Range system 2–0.6 Ma.

The southern closure and Monterey closure biogeographical models were evaluated by comparing their predicted phylogenetic topologies with our Bayesian topology and the associated Bayesian 95% credible set of trees. Our Bayesian topology is not consistent with the Monterey closure model because the coastal clade (*xanthoptica*, *eschscholtzii*) is not recovered as closely related to the inland clade (southern *platensis, croceater*, *klauberi*; cf. Figs 2c & 4a). In the 95% credible set of trees, however, a small number of the topologies (0.08%) recover the coastal and inland clades as sister taxa. This result precludes rigorous rejection of the Monterey closure model. The southern closure model predicts that the coastal and inland clades will be independent and derived from a northern ancestor, and our Bayesian topology, as well as the vast majority (99.92%) of the topologies present in the 95% credible set of trees, are consistent with these criteria (cf. Figs 2a & 4a). We conclude that our data most strongly support the southern closure model of Stebbins (1949).

Mitochondrial DNA haplotype clades and patterns of nuclear differentiation

The current study builds on that of Moritz *et al.* (1992) by identifying several new clades, by resolving much phylogeographical structure within previously known clades, and by advancing our understanding of the geographical distribution of mtDNA haplotype lineages throughout the *Ensatina* complex (Fig. 3). Two new, allopatric lineages were found in *oregonensis* [1], for example, as were new lineages within *xanthoptica*, *eschscholtzii*, northern *platensis* and southern *platensis* (Figs 3 & 4a). In northern California, four separate clades of *oregonensis* ([1–4]) were found, all of which possess substantial phylogeographical structure of their own (Figs 3 & 4a). In addition, a clade representing the subspecies *picta*, and some haplotypes of unclear phylogenetic affinity, are found in northern California. Finally, striking levels of diversity were found in the San Francisco Bay area, including seven supported haplotype lineages within *oregonensis* (see Kuchta *et al.*, 2009 for a detailed consideration of patterns of diversity in central coastal California).

The phylogenetic complexity revealed by our analysis of mtDNA haplotypes is in accordance with early work on patterns of geographical variation in allozymes, which also disclosed notable levels of genetic differentiation (Wake & Yanev, 1986; Jackman & Wake, 1994). For example, Wake & Yanev (1986) examined 19 populations throughout the *Ensatina* complex and found that most populations were separated by large Nei's (1978) genetic distances (*D*), in excess of 0.4 in some comparisons. When we map the results of Wake & Yanev (1986) onto the distribution of haplotype lineages recovered in the current study, we find that where Nei's genetic distances are high, populations represented by separate mtDNA lineages are being compared. For example, Nei's *D* between three populations in northern California ranges from 0.11 to 0.29 (Fig. 5a). Using the terminology of the current study, this corresponds to comparisons between *picta*, *oregonensis* [1] and *oregonensis* [4]. On the other hand, in the few instances in which Nei's *D* is relatively low, comparisons are between populations within single mtDNA haplotype lineages. For instance, Nei's *D* between populations of *eschscholtzii* in Monterey and Santa Barbara County is only 0.03, and both populations are within the range of the northern mtDNA haplotype lineage of *eschscholtzii*.

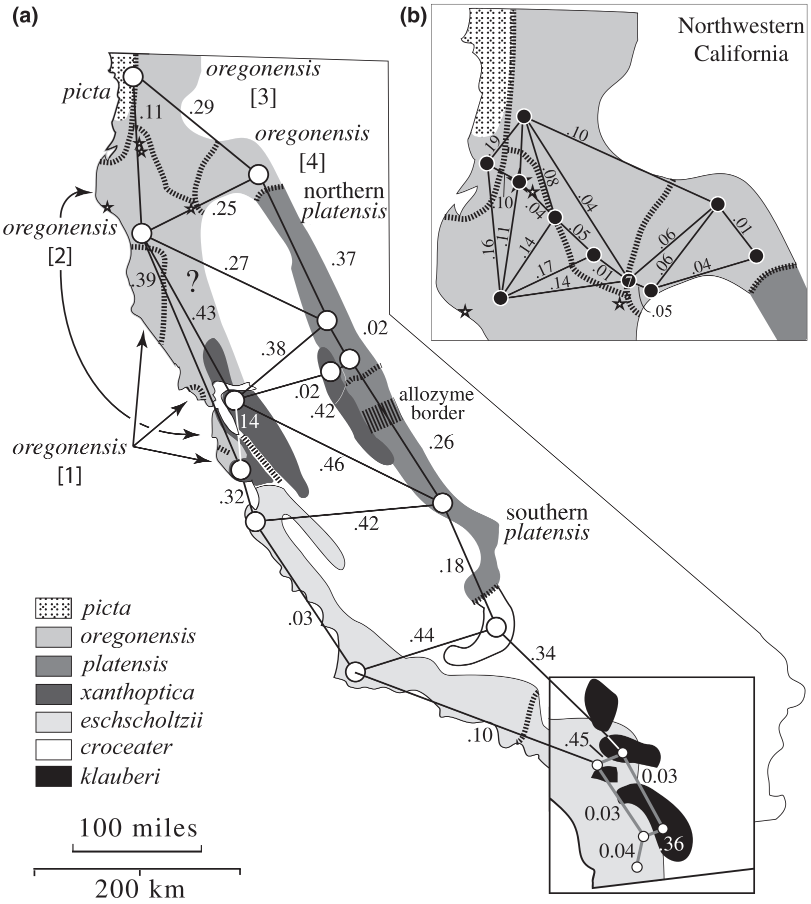


Figure 5 Map illustrating the relationships between previous allozyme studies and the mtDNA clades recovered in the current study. Subspecies are differentially shaded. Within subspecies, the distributions of major mtDNA clades are designated with thick dashed lines. (a) Nei's (1978) genetic distances between samples as reported by Wake & Yanev (1986). The allozymic intergradation zone between northern and southern *platensis* is also shown (Jackman & Wake, 1994). The stars show the location of the northern haplotypes, which are of unclear phylogenetic affinity (Fig. 4a). The question mark in northern California points out an area that we have not sampled for mtDNA, thus we are not confident regarding its phylogenetic affinity. (b) Inset showing an expanded view of northern California. Points show populations studied by Jackman & Wake (1994) (population 7 is labelled because it is referred to specifically in the text); numbers are Nei's (1978) genetic distances between samples.

Given the high levels of phylogeographical structure and the strong pattern of isolation by distance in the *Ensatina* complex (Jackman & Wake, 1994; Kuchta *et al.*, 2009), it is not surprising that the large genetic distances documented by Wake & Yanev (1986) are associated with separate mtDNA clades, because Wake & Yanev (1986) had widely spaced samples (a strategy that made sense given that little was known about genetic diversity in the *Ensatina* complex at the time). Denser sampling is needed to examine patterns of concordance and discordance between allozyme and mtDNA markers (Wake & Schneider, 1998). A first step in this direction can be obtained by examining divergence among populations in northern California, where Jackman & Wake (1994) investigated allozymic differentiation among populations from north western California (*picta*) across the northern end of the Central Valley (*oregonensis* [2–4]) to the northern limit of the Sierra Nevada region (*oregonensis* [4]) (Fig. 5b). They found that Nei's *D* was generally high, ranging up to 0.17 between nearest neighbours within the subspecies *oregonensis*, and isolation by distance characterized the transect. Figure 5b shows how the patterns of allozymic differentiation reported by Jackman & Wake (1994) relate to mtDNA phylogeographical diversity. We see that the allozyme sampling spans four unrelated mtDNA haplotype lineages, suggesting that the high levels of allozyme differentiation are in part a consequence of comparing discrete phylogeographical units. In most instances, however, only a small number of populations (1–4) were sampled for allozymes within the range of each mtDNA lineage, severely hampering comparisons of patterns of variation within vs. between lineages (Fig. 5b). Nonetheless, there is some evidence of admixture where lineages contact one another, as population 7 of Jackman & Wake (1994) was found to contain two sympatric haplotypes belonging to divergent mtDNA lineages (Fig. 5b). In the current study, these haplotypes are assigned to population 7 (*oregonensis* [3]) and population 23 (*oregonensis* [4] Fig. 3). Interestingly, this locality is unremarkable for allozymes, with low Nei's *D* (≤ 0.06) to nearby populations of *oregonensis* [3] and *oregonensis* [4].

Where lineages around the ring meet, such as among lineages of *oregonensis* in northern California, it is necessary to distinguish among the various kinds of evolutionary dynamics that might occur, such as localized hybridization, introgression, or genetic merger. The ring species scenario requires that secondary contacts within the ring are not characterized by reproductive isolation, whereas secondary contacts between the coastal and inland arms must exhibit species-level divergence. In this spirit of assessing contact zone dynamics (Jockusch & Wake, 2002; Alexandrino *et al.*, 2005; Kuchta, 2007), a more rigorous assessment of the association between mtDNA haplotype lineages and patterns of allozymic diversity throughout the *Ensatina* complex has recently been undertaken (Pereira & Wake, in press). Theoretical models suggest that separate mtDNA clades may evolve *in situ* when populations exhibit isolation by distance (cladogenesis without allopatry; Irwin, 2002). If this model is correct (see Templeton, 2004), the *in situ* evolution of discrete mtDNA clades may be an important factor within the *Ensatina* complex, given the low dispersal abilities of *Ensatina* salamanders (Staub *et al.*, 1995) and the strong patterns of isolation by distance that have been documented (Jackman & Wake, 1994; Kuchta *et al.*, 2009).

Ring species and taxonomy

We have focused on the biogeography of the *Ensatina* complex, but there is also a taxonomic dimension to consider. Critics (e.g. Highton, 1998) have argued that the *Ensatina* complex is not special or unusual, but that it is instead comprised of independently evolving species. According to this view, there is no ring species, just inappropriate taxonomy. Highton (1998) thinks recognition of many species – at least 11 – is warranted, using criteria he has developed for species in the plethodontid genus *Plethodon*. Less extreme taxonomic revisions have been proposed. For example, Frost & Hillis (1990) suggested recognizing *klauberi* as a full species because of its allopatric distribution in southern California (Fig. 1a); they also thought the remainder of the complex needs further revision. Graybeal (1995) offered a suggestion for recognizing four species. Highton (1998) argued that no single species could possibly contain so much genetic diversity as that recorded in *Ensatina* (and he did not consider the results published by Wake, 1997). Wake & Schneider (1998) countered by reviewing much of the complexity in *Ensatina*, including numerous instances of discordance among morphological, allozymic and mtDNA sets, and argued that Highton (1998) was using a phenetic (as opposed to phylogenetic) methodology that artificially sharpened the borders between units that lack evidence of genetic and evolutionary independence. The pattern of haplotype clade distributions presented in this paper portrays a patchwork of exclusive geographical ranges. However, it is simplistic to consider these haplotype clades to be full species, despite the parapatric nature of the ranges and the near absence of sympatry except in contact zones. There are discordances between patterns in the mtDNA clades and patterns based on allozymes and coloration (Wake & Schneider, 1998). The stage is now set for in-depth analyses of the regions of discordance, which will entail the use of multiple molecular markers (e.g. projects in progress by T. Devitt and R. Pereira). Pending results of such studies, we continue to accept the taxonomy of Stebbins (1949) as the best available alternative. Of the seven recognized subspecies, *xanthoptica*, *eschscholtzii*, *klauberi* and *croceater* are potentially genealogical entities, monophyletic or nearly so with respect to all three kinds of data. Both *oregonensis* and *platensis* are recognizable as originally diagnosed by Stebbins (1949), but each is di- to polyphyletic with respect to mtDNA, and they are sufficiently complex with respect to allozymes that it seems safe to assume that neither is a genealogical unit. The subspecies category is controversial; there is no general agreement that subspecies must or should be monophyletic. Instead, their utility is to provide labels for phenotypically recognizable, geographically discrete segments of complexes of species that remain under study (Wake & Schneider, 1998; Manier, 2004; Mulcahy, 2008). Examples in addition to *Ensatina* among salamanders include the *Ambystoma tigrinum*, *Salamandra salamandra* and *Bolitoglossa franklini* complexes (Wake & Lynch, 1982; Shaffer & McKnight, 1996; Steinfartz *et al.*, 2000). Until definitive evidence for the evolutionary independence of components of the *Ensatina* complex warrants a taxonomic revision (using diverse criteria within the framework of the general lineage species concept; de Queiroz, 1998), we recommend continuation of the now familiar and utilitarian taxonomy first proposed by Stebbins (1949). We prefer to direct attention towards what the complex has to teach us about the diversification process, as well as the limits of the species category itself.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Population numbers, collecting localities, Museum of Vertebrate Zoology (MVZ) accession numbers, identifications of sequences used in analyses, and GenBank accession numbers.

BIOSKETCH

Research in the Museum of Vertebrate Zoology (MVZ) is centred on evolutionary biology from the perspectives of systematics, ecology, behaviour, functional and developmental morphology, population biology, and evolutionary genomics. In addition, the MVZ aims to lead the way in developing and using natural history collections for research, education and problems in biodiversity conservation. S.R.K., D.S.P. and R.L.M. are all former graduate students under D.B.W. Members of the Wake group study how diversity is generated through time and space, with a particular research focus on salamanders. S.R.K., D.S.P. and D.B.W. conceived the ideas and collected the data; S.R.K. and R.L.M. conducted the analyses; the manuscript was written by S.R.K. and D.B.W.

Editor: Brett Riddle

Appendix S1 Locality information for *Ensatina eschscholtzii* samples. Population numbers correspond to Figure 3, and are used throughout the text. Samples within 1 km that contain haplotypes belonging to the same clade are grouped into single populations. MVZ#: Accession number for the Museum of Vertebrate Zoology, University of California, Berkeley. Major clades and clades are discussed in the manuscript text.

Population	**MVZ #**	**Longitude**	**Latitude**	**Locality**	**County**	**Subspecies**	**Major Clade**	**Clade**	**Genbank**
0a	168659	-121.93490	48.09610	1 mi ENE Granite Falls at Wayside Mine	Snohomish Co, WA	*oregonensis*	clade A[1]	*oregonensis* [3]	L75811
0b	167999	-123.63130	45.77390	Nehalem River Rd., Clatsop-Tillamook County line	Clatsop, OR	*oregonensis*	clade A	*oregonensis* [3]	FJ151653
0c	222558	-123.54890	44.50280	Mary's Peak, 1.1 mi W Hwy. 201, U.S. Forest Service 3406	Benton, OR	*oregonensis*	clade A	*oregonensis* [3]	FJ151654
0d	219754	-122.23460	44.02110	Hidden Lake	Lane, OR	*oregonensis*	clade A	*oregonensis* [3]	FJ151655
0e	172504	-123.65180	43.89860	W Fork Road, 15.5 mi S confluence of Wolf Creek and Siuslaw River	Douglas, OR	*oregonensis*	clade A	*oregonensis* [3]	FJ151656
0f	168668	-122.20880	43.60470	Wolf Creek Rd.	Lane Co, OR	*oregonensis*	clade A	*oregonensis* [3]	L75810
0g	218043	-122.58370	43.11730	Carmen Lake above Camp Comfort, Umpqua National Forest	Douglas, OR	*oregonensis*	clade A	*oregonensis* [3]	FJ151657
0h	168679	-123.26010	42.90790	ca. 1 mi S Canyonville along Canyon Drive	Douglas, OR	*oregonensis*	clade A	*oregonensis* [3]	FJ151658
0i	167244	-124.30610	42.12010	Carpenterville Hwy. [Old 101], 7.7 mi N junction Hwy. 101	Curry, OR	*oregonensis*	clade A	*oregonensis* [3]	FJ151659
1	182055	-123.14100	41.90500	Seiad Creek Valley, 5.7 - 5.9 mi NE Hwy 96 at Seiad Valley	Siskiyou	*oregonensis*	clade A	*oregonensis* [3]	FJ151660
2	219715	-123.36700	41.88700	On Jackson Peak 8.3 mi N on Forest Rd 19NO1 from Hwy 96	Siskiyou	*oregonensis*	clade A	*oregonensis* [3]	FJ151661
3a[‡]	191695	-123.89863	41.71281	Hurdygurdy Creek, 0.4 mi S Hurdygurdy Bridge	Del Norte	*oregonensis*	clade A	*oregonensis* [3]	FJ151662
3b	191697	-123.89863	41.71281	Ibid.	Del Norte	*oregonensis*	clade A	*oregonensis* [3]	FJ151663
3c	191698	-123.89863	41.71281	Ibid.	Del Norte	*oregonensis*	clade A	*oregonensis* [3]	FJ151664
4	182066	-123.50350	41.36720	Ishi Pishi Rd., 1.0 mi S Somes Bar	Humboldt	*oregonensis*	clade A	*oregonensis* [3]	FJ151665
5	215747	-122.34800	41.05470	S slope Hazel Creek, 0.8 mi SE Sacramento River	Shasta	*oregonensis*	clade A	*oregonensis* [3]	FJ151666
6	215826	-123.12870	40.77470	E Fork Rd., N 299 at Helena	Trinity	*oregonensis*	clade A	*oregonensis* [3]	L75807
7	233091	-122.98056	40.73972	East slope of Oregon Mt, 2.5 mi W of Weaverville on Hwy 299	Trinity	*oregonensis*	clade A	*oregonensis* [3]	FJ151667
8	182090	-123.39366	41.78398	Little Grider Creek, Hwy. 96	Siskiyou	*oregonensis*	clade A	*oregonensis* [3]	FJ151668
9	172513	-124.07729	41.85456	Low Divide Rd., 3.3 mi N junction Hwy. 197	Del Norte	*picta*	clade A	*picta*	L75815

Population	MVZ #	Longitude	Latitude	Locality	County	Subspecies	Major Clade	Clade	Genbank
10a	220618	-124.01813	41.75281	NE slope Bald Hill, 3.5 mi SE jct Hwy 199 and South Fork Rd	Del Norte	*picta*	clade A	*picta*	FJ151669
10b	220619	-124.01813	41.75281	Ibid.	Del Norte	*picta*	clade A	*picta*	FJ151670
10c	220620	-124.01813	41.75281	Ibid.	Del Norte	*picta*	clade A	*picta*	FJ151671
11	168709	-124.09109	41.61493	Wilson Creek Rd., 0.8 mi NE Hwy. 101	Del Norte	*picta*	clade A	*picta*	L75815
12	167286	-124.15257	41.12158	1.0 mi S Patrick's State Park by U.S. 101	Humboldt	*picta*	clade A	*picta*	FJ151672
13	237526	-123.62400	40.93940	off Hwy 299, 0.4 mi E of jct. with Hwy 96, Willow Creek	Humboldt	*oregonensis*	clade A	northern haplotype	FJ151673
14	220597	-123.86730	40.90990	Snow Camp Rd, 1.4 mi S Hwy 299 at Lord-Ellis Summit	Humboldt	*picta*	clade A	*picta*	FJ151674
15	215802	-123.54194	40.88139	Rest area, 2.5 mi SE Salyer	Trinity	*oregonensis*	clade A	northern haplotype	FJ151675
16	195651	-123.87429	40.75823	Jct. Of Butter Valley Road and Maple Creek Road	Humboldt	*picta*	clade A	*picta*	FJ151676
17‡	211881	-124.20910	40.19190	Kinsey Ridge, near Headwaters of Wild Oat Creek	Humboldt	*oregonensis*	clade A	northern haplotype	FJ151677
18	219676	-122.23750	40.92472	2.2 mi SSE McCloud Rd. Bridge, Bollibakka Mt. region	Shasta	*oregonensis*	clade A	oregonensis [4]	FJ151678
19	219674	-122.20722	40.91139	Nosoni Creek at Rd. 27 Bridge	Shasta	*oregonensis*	clade A	oregonensis [4]	FJ151679
20	197522	-121.72091	40.88276	~3 mi W Burney	Shasta	*oregonensis*	clade A	oregonensis [4]	FJ151680
21a‡	SRK 1969^2	-122.25430	40.87380	Gilman Rd.	Shasta	*oregonensis*	clade A	oregonensis [4]	FJ151681
21b	SRK 1971^2	-122.28450	40.87850	Ibid.	Shasta	*oregonensis*	clade A	oregonensis [4]	FJ151682
22	182000	-122.00388	40.77578	6.2 mi NE Ingot, Hwy. 299	Shasta	*oregonensis*	clade A	oregonensis [4]	L75808
23	233089	-122.98056	40.73972	East slope of Oregon Mt, 2.5 mi W of Weaverville on Hwy 299	Trinity	*oregonensis*	clade A	oregonensis [4]	FJ151683
24	SRK 1970	-122.30790	40.72910	Fawndale Rd., near locked gate, Mountain Limestone Quarry	Shasta	*oregonensis*	clade A	oregonensis [4]	FJ151684
25	S10997	-122.88800	40.68100	Poker Bar Rd.	Trinity	*oregonensis*	clade A	oregonensis [4]	FJ151685
26	S10793	-121.83530	40.52630	1 mi W of Shingletown Airport & 1.5 mi N Hwy 44	Shasta	*oregonensis*	clade A	oregonensis [4]	FJ151686
27	237552	-122.90900	40.70500	0.2 mi down Browns Mt Rd, Little Browns Creek Rd, E of Weaverville	Trinity	*oregonensis*	clade A	northern haplotype	FJ151687
28	220589	-124.03046	40.52612	1.6 mi E Carlotta on Hwy 36	Humboldt	*oregonensis*	clade A	*oregonensis* [2]	FJ151688
29	158076	-123.61220	40.17870	Alderpoint	Humboldt	*oregonensis*	clade A	*oregonensis* [2]	FJ151689
30	181357	-123.99400	40.09500	3 mi S Ettersberg	Humboldt	*oregonensis*	clade A	*oregonensis* [2]	FJ151690
31a	182034	-123.71750	39.85694	Drive-thru Tree, Leggett	Mendocino	*oregonensis*	clade A	*oregonensis* [2]	FJ151691
31b	182035	-123.71750	39.85694	Drive-thru Tree, Leggett	Mendocino	*oregonensis*	clade A	*oregonensis* [2]	FJ151692
32	194159	-122.83330	38.70000	1.5 mi N Hwy. 128 on Geysers Rd.	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151693

Population	**MVZ #**	**Longitude**	**Latitude**	**Locality**	**County**	**Subspecies**	**Major Clade**	**Clade**	**Genbank**
33	158159	-123.10830	38.68330	Skaggs Springs Rd., 1.3 mi E Las Lomas	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151694
34	238155	-122.59617	38.64148	0.35 mi S of Lawton/Old Toll Rd, on Hwy 29, N of Calistoga	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151695
35	208381	-122.77500	38.62500	Maacama Cr., 1.3 mi S Hwy 128 on CHalk Hill Rd.	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151696
36	221138	-123.15830	38.61670	Jim Creek	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151697
37a	217497	-122.91974	38.59070	Mill Creek Rd., ca. 3 mi W Woodside Rd., WSW Healdsburg	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151698
37b	217502	-122.91974	38.59070	Ibid.	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151699
38a	237529	-122.84617	38.60488	Bailhache Ave., S side of Russian, Healdsburg	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151700
38b	237530	-122.84617	38.60488	Ibid.	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151701
39	238160	-122.64426	38.60272	0.1 mi W of Napa Co. Line on Hwy 128, N of Calistoga	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151702
40	238157	-122.61980	38.58413	1 mi up Franz Valley School Rd, off Petrified Forest Rd, N of Calistoga	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151703
41	237531	-122.69417	38.58333	Pepperwood Ranch Natural Preserve, N of Franz Valley Rd	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151704
42	226755	-122.76700	38.57500	Chalk Hill Rd., 0.7 mi S Spurgeon Rd. and 2.7 mi N Leslie Rd.	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151705
43	226752	-122.61700	38.55000	0.1 mi W on Lorraine Rd, 0.2 mi W Mark West Spring Rd, Santa Rosa	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151706
44	226051	-122.71917	38.54222	along Mark W Spr. Rd., ca. 0.5 mi S Mark W. Resort	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151707
45a	188992	-122.39684	38.50527	ca. 5.0 mi E St. Helena along Conn Valley Rd.	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151708
45b	238164	-122.59182	38.52068	4.1 miles down St. Helena Rd., W of Calistoga Rd., near Calistoga	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151709
46	221126	-122.93300	38.51700	McPeak Rd., 0.6 mi NW River Rd., at Crossing of Russian River	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151710
47[‡]	221086	-122.91667	38.51667	Canyon Rd., 0.3 mi SSW River Rd., Hollydale	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151711
48a	226053	-122.88333	38.50806	W. side Wohler Rd. Bridge	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151712
48b	226054	-122.88389	38.50944	Hill 200 m NW end Wohler Rd. Bridge	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151713
49	188994	-122.39684	38.50527	ca. 5.0 mi E (by road) St. Helena along Conn Valley Rd.	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151714
50	226745	-122.90900	38.47300	0.1 mi S Hwy. 116 on Giovanetti Rd.	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151715
51a	158111	-122.24253	38.43349	NE side Atlas Peak, 9 mi on Atlas Peak Rd. from Hwy. 121	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151716

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51b	205516	-122.61670	38.46670	0.3 mi E of Los Alamos Rd. on Wildwood Rd. near Santa Rosa	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151717
52	226760	-122.92472	38.44778	Green Valley Road, 200 ft E Harrison Grade Road, E Graton	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151718
53	158112	-122.24253	38.43349	NE side Atlas Peak, 9 mi (by road) on Atlas Peak Rd. from Hwy. 121	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151719
54	211897	-122.91670	38.41670	0.6 mi W Green Hill Rd. on Graton road along Parrington Creek	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151720
55	208426	-122.86670	38.40000	0.8 mi N of Bodega Hwy. on Ferguson Rd.	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151721
56	237565	-122.85000	38.36700	Kennedy Rd, 1 mi E of jct of Burnside Rd, Sebastapol	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151722
57	205514	-122.45800	38.37500	6.6 mi NE of Hwy 12 on Cavedale Rd.	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151723
58	237500	-122.41083	38.36871	Mt. Veeder Rd, 4.05 mi N of Redwood Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151724
59	237501	-122.38616	38.35919	Mt. Veeder Rd, 2.2 mi N of Redwood Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151725
60a	237495	-122.38274	38.35533	Mt. Veeder Rd, 1.85 mi N of Redwood Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151726
60b	237496	-122.38451	38.35757	Mt. Veeder Rd, 2.05 mi N of Redwood Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151727
60c	237497	-122.38451	38.35757	Ibid.	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151728
60d	237498	-122.38451	38.35757	Ibid.	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151729
60e	237499	-122.38451	38.35757	Ibid.	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151730
60f	237502	-122.38451	38.35757	Ibid.	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151731
60g	238159	-122.38370	38.35643	Mt. Veeder Rd, 1.95 mi N of Redwood Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151732
61	237516	-122.41921	38.34754	Redwood Rd., 3.45 mi W of Mt Veeder Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151733
62a	237519	-122.39843	38.34512	Redwood Rd., 2.1 mi W of Mt Veeder Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151734
62b	237523	-122.39843	38.34512	Ibid.	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151735
63	237558	-122.86100	38.34500	English Hill, 1.6 mi S Barnett Valley Rd on Burnside Rd	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151736
64	237514	-122.40065	38.34492	Redwood Rd., 2.25 mi W of Mt Veeder Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151737
65a	237515	-122.41312	38.34416	Redwood Rd., 3.0 mi W of Mt Veeder Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151738
65b	237517	-122.40990	38.34464	Redwood Rd., 2.8 mi W of Mt Veeder Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151739
65c	237518	-122.40318	38.34416	Redwood Rd., 2.4 mi W of Mt Veeder Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151740
66	237513	-122.39271	38.34174	Redwood Rd., 1.7 mi W of Mt Veeder Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151741
67a	237520	-122.38029	38.33457	Redwood Rd., 0.7 mi W of Mt Veeder Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151742
67b	237521	-122.37523	38.33450	Redwood Rd., 0.4 mi W of Mt Veeder Rd	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151743
67c	237522	-122.37523	38.33450	Ibid.	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151744
68	237494	-122.34550	38.32090	Mt. Veeder Rd, 0.75 mi N Browns Valley Rd, W town of Napa	Napa	*oregonensis*	clade A	*oregonensis* [2]	FJ151745

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69	237549	-122.39847	38.29623	Lovall Valley Rd, ~0.7 mi E of jct with Wood Valley Rd	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151746
70	237532	-122.39812	38.29478	Lovall Valley Rd, ~0.6 mi NW of the jct. with Lovall Valley Loop Rd	Sonoma	*oregonensis*	clade A	*oregonensis* [2]	FJ151747
71a	Tissue only[3]	-122.94740	38.17920	Tomales Point, 1200 m southwest end of road	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151748
71b	Tissue only[3]	-122.94740	38.17920	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151749
72*	226727	-122.62803	38.12075	0.1 mi E entrance Indian Valley Golf Club off Navato Rd, Navato	Marin	*xanthoptica*	coastal lineage	*xanthoptica* [1]	*
73a	237144	-122.83840	38.10470	Along Hwy 1 at E margin Tomales Bay	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151751
73b	237145	-122.83840	38.10470	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151752
74a	Tissue only[3]	-122.87930	38.09920	1.1 km SE jct Sir Frances Drake Hwy & Pierce Point Rd	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151753
74b	Tissue only[3]	-122.87930	38.09920	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151754
74c	Tissue only[3]	-122.87930	38.09920	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151755
74d	Tissue only[3]	-122.87930	38.09920	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151756
74e	Tissue only[3]	-122.88400	38.09500	Point Reyes, 1.9 km SE jct. Sir Francis Drake Hwy & Pierce Pt Rd	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151757
75a	Tissue only[3]	-122.88250	38.09350	1.9 km SE jct Sir Frances Drake Hwy & Pierce Point Rd	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151758
75b	Tissue only[3]	-122.88250	38.09350	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151759
75c	Tissue only[3]	-122.88250	38.09350	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151760
75d	Tissue only[3]	-122.88250	38.09350	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151761
75e	Tissue only[3]	-122.88250	38.09350	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151762
75f	Tissue only[3]	-122.88070	38.08830	Mt. Vision, 2.1 km SE jct Sir Frances Drake Hwy & Pierce Point Rd.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151763
75g	Tissue only[3]	-122.88070	38.08830	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151764
75h	Tissue only[3]	-122.88070	38.08830	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151765
75i	Tissue only[3]	-122.88070	38.08830	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151766
75j	Tissue only[3]	-122.88070	38.08830	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151767
76a	Tissue only[3]	-122.86890	38.02340	Coast Trail, 7.2 km WSW of Olema, Point Reyes National Seashore	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151768

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76b	Tissue only[3]	-122.86890	38.02340	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151769
77a	219633	-122.68323	38.00814	S end Montezuma Rd., 0.5 mi S Sir Francis Drake Blvd., Forest Knolls	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151770
77b	219634	-122.68323	38.00814	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151771
78	220624	-122.60359	37.97221	below Sky Oaks Rd., E junction with Bolinas Rd.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151772
79a‡	Tissue only[3]	-122.69820	37.96970	Bolinas Ridge Trail, 4 km N of intersection of Hwy 1 & road into Bolinas	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151773
79b	Tissue only[3]	-122.69820	37.96970	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151774
80a	237491	-122.44851	37.88854	Paradise Dr, ~3.1 mi S from jct with Trestle Glen Blvd	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151775
80b	237492	-122.44851	37.88854	Ibid.	Marin	*oregonensis*	clade A	*oregonensis* [2]	FJ151776
81	185818	-122.42127	37.49490	Digger Canyon, 1.5 mi N Pilarcitos Cr on Apanolio Cr, Half Moon Bay	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151777
82	222995	-122.33722	37.45801	Skyline Blvd, 3.8 mi S of Hwy. 92	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151778
83	230800	-122.28945	37.42927	King's Mountain Rd., 1.9 mi W Tripp Rd.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151779
84*	223008	-122.31917	37.42016	Tunitas Creek Rd., 0.75 mi S of Skyline Blvd.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	*
85	215831	-122.26035	37.39841	Alembique Creek at Crossing of Hwy. 84, S of Woodside	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151780
86*	222993	-122.25306	37.37186	Skyline Blvd., 1.4 mi S of CA 84	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	*
87a	230782	-122.33917	37.34417	Bear Gulch Rd., 1.5 mi N junction 84	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151781
87b	230783	-122.33917	37.34417	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151782
88a	222987	-122.18600	37.31510	Skyline Blvd. at Alpine Rd.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151783
88b	222988	-122.18600	37.31510	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151784
88c‡	222989	-122.18600	37.31510	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151785
88d	222990	-122.18600	37.31510	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151786
88e	222991	-122.18600	37.31510	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151787
88f	222992	-122.18600	37.31510	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151788
89	230785	-122.26694	37.30528	Junction of Pescadero Rd. and Boys school Rd.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151789
90a	230786	-122.28417	37.28556	Pescadero Rd., 10 mi E Hwy. 1	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151790
90b	230889	-122.28056	37.29167	Pescadero Rd., 0.7 mi N Warr Rd.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151791
90c	230890	-122.28056	37.29167	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151792
90d	230891	-122.28056	37.29167	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151793
90e	230892	-122.28056	37.29167	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151794
90f	230893	-122.28056	37.29167	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151795
90g	230894	-122.28056	37.29167	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151796

Population	MVZ #	Longitude	Latitude	Locality	County	Subspecies	Major Clade	Clade	Genbank
90h	230895	-122.28056	37.29167	Ibid.	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	FJ151797
91*	230778	-122.21056	37.26778	Portola State Park Rd. at North entrance of Portola State Park	San Mateo	*oregonensis*	clade A	*oregonensis* [2]	*
92*	223016	-122.12889	37.26111	Skyline Blvd., 13.1 mi S of Hwy. 84	Santa Cruz	*oregonensis*	clade A	*oregonensis* [2]	*
93	230838	-122.15092	37.21131	CA 9, 0.25 mi E of jct. CA 236	Santa Cruz	*oregonensis*	clade A	*oregonensis* [2]	FJ151798
94	194081	-123.48519	39.68634	Branscomb Rd., 9.7 mi W Hwy. 101 at Laytonville	Mendocino	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	L75806
95[‡]	237548	-123.23542	39.39033	Noyo River, 0.25 mile E Old Union Lumber Rd in Jackson State Forest	Mendocino	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151799
96	237547	-123.65803	39.35420	N Hwy 20 at Parlin Fork Conservation Camp exit in Jackson State Forest	Mendocino	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151800
97[†]	168991	-123.67861	39.17972	Hwy. 128, Barton Gulch, 4.3 mi SE Hwy. 1	Mendocino	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151801
98	194896	-123.54166	39.15260	1.9 mi NW Clark Rd., near Navarro	Mendocino	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	L75809
99	221131	-123.43583	38.70333	Sea Ranch, 1.2 mi E Hwy. 1, on Lookout Rd.	Sonoma	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151802
100a	Tissue only[3]	-122.80230	38.01230	Bear Valley Trail, 3.3 km SSW of Olema, Point Reyes National Seashore	Marin	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151803
100b	Tissue only[3]	-122.80230	38.01230	Ibid.	Marin	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151804
100c	Tissue only[3]	-122.80230	38.01230	Ibid.	Marin	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151805
100d	Tissue only[3]	-122.80300	38.01200	Point Reyes, Bear Valley, 0.8 km S Divide Meadow, 3.3 km SSW Olema	Marin	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151806
100e	Tissue only[3]	-122.80140	38.01050	Bear Valley Trail, 3.3 km SSW of Olema, Point Reyes National Seashore	Marin	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151807
100f	Tissue only[3]	-122.80140	38.01050	Ibid.	Marin	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151808
100g	Tissue only[3]	-122.80140	38.01050	Ibid.	Marin	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151809
100h	Tissue only[3]	-122.80140	38.01050	Ibid.	Marin	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151810
101	Tissue only[3]	-122.76360	38.00500	Olema Creek, 1 km NW 5-Brook	Marin	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151811
102[‡]	Tissue only[3]	-122.77500	37.99300	Point Reyes, Steward Trail at jct. Greenpicker Trail, 5.2 km S of Olema	Marin	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151812
103	Tissue only[3]	-122.77420	37.99150	Stewart Trail, 5.2 km S of Olema, Point Reyes National Seashore	Marin	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151813
104a	230774	-122.31972	37.26611	Pescadero Creek Rd., 6.7 mi E jct. Hwy. 1	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151814
104b	230775	-122.31972	37.26611	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151815
104c	230776	-122.31972	37.26611	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151816
104d	230792	-122.31613	37.27007	Pescadero Creek Rd., 7 mi E jct. Hwy 1	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151817

Population	MVZ #	Longitude	Latitude	Locality	County	Subspecies	Major Clade	Clade	Genbank
104e	230793	-122.31613	37.27007	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151818
104f	230794	-122.31613	37.27007	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151819
104g	230795	-122.31613	37.27007	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151820
104h	230796	-122.31613	37.27007	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151821
104i	230797	-122.31613	37.27007	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151822
104j	230798	-122.31613	37.27007	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151823
104k	230799	-122.31613	37.27007	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151824
105a	226735	-122.33089	37.22403	Butano Park Rd., 1.4 mi E jct Cloverdale Rd	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151825
105b	226736	-122.33089	37.22403	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151826
105c	226737	-122.33089	37.22403	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151827
105d	230801	-122.33089	37.22403	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151828
105e	230802	-122.33089	37.22403	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151829
105f	230803	-122.33089	37.22403	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151830
105g	230804	-122.33089	37.22403	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151831
106a	230779	-122.28056	37.22250	Butano Fire Trail at East Boundary, Butano State Park	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151832
106b	230863	-122.28056	37.22250	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151833
107	230864	-122.19200	37.19200	Hwy. 236, 2.7 mi SW junction Hwy 9 (N junction)	Santa Cruz	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151834
108a	230780	-122.32889	37.18694	Gazos Creek Rd., 1 mi E of Cloverdale	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151835
108b‡	230781	-122.32889	37.18694	Ibid.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151836
109	230790	-122.26700	37.10800	Skyline-to-Sea Trail at Tramway spring, 1.5 mi N Hwy. 1	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151837
110	226738	-122.29150	37.10780	Hwy. 1 at border beween Santa Cruz & San Mateo Co.	San Mateo	*oregonensis*	*oregonensis* [1]	*oregonensis* [1]	FJ151838
111	208454	-122.76670	38.55000	0.4 mi E of Chalk Hill Rd. on Leslie Rd.	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151839
112	208456	-122.74200	38.50800	0.3 mi N of Mark West Creek Rd on Wikiup Bridgeway Rd	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151840
113	237577	-122.88000	38.50720	East side of Wohler Bridge	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151841
114	226750	-122.84400	38.48500	0.5 mi W Laguna Rd., 0.1 mi E River Rd., Trenton Rd., Forestville	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151842
115a	205681	-122.70000	38.48300	0.4 mi E Parker Hill road along Pine Creek, Santa Rosa	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	L75819
115b	205686	-122.70000	38.48300	Ibid.	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151843

Population	MVZ #	Longitude	Latitude	Locality	County	Subspecies	Major Clade	Clade	Genbank
116	226761	-122.85800	38.46700	Vine Hill School Rd., 0.1 mi E Vine Hill Rd., N Graton	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151844
117	217519	-122.70830	38.45000	Santa Rosa Junior College	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151845
118	208457	-122.85000	38.44170	0.6 mi N of Hwy. 116 on Frei Rd.	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151846
119	237579	-122.83200	38.42200	200 meters S Occidental Rd on High School Rd, Sebastapol	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151847
120	237576	-122.82833	38.41389	1708 Hurlbut Dr, N of Sebastapol	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151848
121	215907	-122.64170	38.38330	0.2 mi W F Grange Rd. on Peracca Rd.	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151849
122	205023	-122.60800	38.36700	1.2 mi E of Pressley Rd. on Sonoma Mt. Rd.	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151850
123	237587	-122.56750	38.36610	0.5 mi W of Enterprise Rd on Sonoma Mountain Rd	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151851
124	237586	-122.57639	38.36528	1.1 mi W of Enterprise Rd on Sonoma Mountain Rd	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151852
125	237584	-122.54250	38.35528	Near Entrance to Jack London Regional Park, London Ranch Rd	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151853
126	237581	-122.58280	38.33230	End of Sonoma Mt. Rd., near Peak of Sonoma Mt	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151854
127	222976	-122.35373	38.33043	1.8 mi W Napa, 2930 Redwood Rd.	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151855
128a	237511	-122.36382	38.31476	Patrick Rd., 2.0 mi W Brown's Valley Rd., W of Napa	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151856
128b	237512	-122.36382	38.31476	Ibid.	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151857
129a	181413	-122.34883	38.31152	3.2 mi W of Napa on Patrick Rd.	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151858
129b	237503	-122.34942	38.31186	Patrick Rd., 1.0 mi W Brown's Valley Rd.	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151859
129c	237505	-122.35029	38.31310	Patrick Rd., 1.1 mi W Brown's Valley Rd.	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151860
129d	237506	-122.35160	38.31352	Patrick Rd., 1.2 mi W Brown's Valley Rd.	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151861
129e	237507	-122.35492	38.31352	Patrick Rd., 1.4 mi W Brown's Valley Rd.	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151862
129f	237508	-122.36007	38.31262	Patrick Rd., 1.7 mi W Brown's Valley Rd.	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151863
129g	237509	-122.36077	38.31228	Patrick Rd., 1.75 mi W Brown's Valley Rd.	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151864
129h	237510	-122.36077	38.31228	Ibid.	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151865
130	237585	-122.60939	38.30962	Lynch Rd, 0.6 mi E of jct. with Hardin Lane, Sonoma Mt.	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151866
131a	237588	-122.54880	38.30840	Spring Rd, 0.4 mi from Prospect Rd & 0.5 mi from Grove Rd	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151867
131b	237589	-122.54880	38.30840	Ibid.	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151868
132a	237582	-122.62268	38.30217	Hardin Lane, 0.7 mi W of jct with Lynch Rd	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151869
132b‡	237583	-122.62268	38.30217	Ibid.	Sonoma	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151870

Population	MVZ #	Longitude	Latitude	Locality	County	Subspecies	Major Clade	Clade	Genbank
133	236229	-122.37222	38.25389	ca. 0.4 mi E of the Sonoma/Napa Co border on Hwy 12	Napa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151871
134	237574	-122.22160	37.89840	Near jct Wildcat Canyon Rd and El Toyonal Rd	Alameda	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151872
135a	237566	-122.21750	37.89180	El Toyonal Rd, between Wildcat Canyon Rd and Chapparal Place	Alameda	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151873
135b	237567	-122.21750	37.89180	Ibid.	Alameda	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151874
135c	237568	-122.21750	37.89180	Ibid.	Alameda	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151875
135d	237569	-122.21750	37.89180	Ibid.	Alameda	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151876
135e	237571	-122.21750	37.89180	Ibid.	Alameda	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151877
135f	237572	-122.21750	37.89180	Ibid.	Alameda	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151878
135g	237573	-122.21750	37.89180	Ibid.	Alameda	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151879
136	163850	-122.17544	37.87184	35 Glorietta Ct., Orinda	Contra Costa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	L75818
137	215743	-121.69975	37.71810	at junction of 580 and Greenville Rd., E of Livermore	Alameda	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151880
138	CAS 20748[4]	-122.45000	37.69200	Guadalupe Cyn Pkwy, 0.1 mi W of entrance San Bruno Mtn. State Park	San Mateo	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151881
139	215891	-121.95000	37.68330	Upper Reaches of de Vaney Canyon	Alameda	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151882
140	167291	-122.33541	37.55555	0.7 mi W El Camino Real, Crystal Spr. Rd. at Cunningham Way	San Mateo	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151883
141	230770	-121.41025	36.97050	Lone Tree Rd., circa 8 mi E Fairview Rd.	San Benito	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151884
142	243224	-120.54672	38.36290	Wolverine Mine Rd., 2.1 mi ENE Glencoe	Calaveras	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151885
143a	243142	-120.59322	38.35962	0.8 mi NW Glencoe	Calaveras	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151886
143b	243143	-120.59322	38.35962	Ibid.	Calaveras	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151887
143c	243145	-120.59322	38.35962	Ibid.	Calaveras	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151888
144[‡]	243217	-120.54497	38.35047	Wet Gulch-Fir Transect, 2.2 mi E Glencoe	Calaveras	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151889
145	202316	-120.46400	38.17290	0.9 mi E Fullen Rd. on Sheep Ranch Rd.	Calaveras	*xanthoptica*	coastal lineage	*xanthoptica* [1]	L75817
146a	236230	-120.18917	37.76889	Cuneo Rd at Jackass Creek Access Rd	Mariposa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151890
146b	236231	-120.18917	37.76889	Ibid.	Mariposa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151891
147	236233	-120.14917	37.73778	Greeley Hill Divide on Hwy J 132 ca 1 mi W Greeley Hill Village	Mariposa	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151892
148a	244099	-119.63020	37.39500	Lewis Fork Creek, SE of intersection of Deer Run Trail & Cedar Valley Rd.	Madera	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151893
148b	244100	-119.63020	37.39500	Ibid.	Madera	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151894
148c	244101	-119.63020	37.39500	Ibid.	Madera	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151895

Population	MVZ #	Longitude	Latitude	Locality	County	Subspecies	Major Clade	Clade	Genbank
149a	244090	-119.64740	37.30500	Potter Ridge, S Oakhurst, 0.7 mi N Hwy. 41 on Fresno Flats Rd.	Madera	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151896
149b	244091	-119.64740	37.30500	Ibid.	Madera	*xanthoptica*	coastal lineage	*xanthoptica* [1]	FJ151897
150a	230866	-122.19200	37.19200	Hwy. 236, 2.7 mi SW junction Hwy 9 (N junction)	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151898
150b	230867	-122.19200	37.19200	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151899
151	230816	-121.96700	37.18300	Soda Springs Rd., 0.4 mi E Alma Bridge Rd.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151900
152	230787	-122.11700	37.18300	Kings Creek Rd., 2.6 mi N junction Hwy 9	San Mateo	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151901
153a	230870	-122.19200	37.17500	Lodge Rd., 1.1 mi N junction Hwy. 236	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151902
153b	230871	-122.19200	37.17500	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151903
153c	230872	-122.19200	37.17500	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151904
153d	230873	-122.19200	37.17500	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151905
153e	230877	-122.19200	37.17500	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151906
153f	230878	-122.19200	37.17500	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151907
153g	230879	-122.19200	37.17500	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151908
153h	230880	-122.19200	37.17500	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151909
153i	230881	-122.19200	37.17500	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151910
153j	230882	-122.19200	37.17500	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151911
153k	230883	-122.19200	37.17500	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151912
153l	230884	-122.19200	37.17500	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151913
154	223015	-122.06889	37.16972	Bear Creek Rd., 4.9 mi E of Hwy. 9	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151914
155*	223018	-122.13583	37.16639	Hwy. 9, 4.5 mi S of Hwy. 236	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	*
156a	230868	-122.20000	37.15800	Little Basin Rd., 1.3 mi S junction Hwy. 236	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151915
156b	230869	-122.20000	37.15800	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151916
157a	230817	-121.94200	37.12500	Morrill Rd., 0.2 mi W junction Wrights Station Rd.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151917
157b	230818	-121.94200	37.12500	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151918
157c	230819	-121.94200	37.12500	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151919
157d	230821	-121.94200	37.12500	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151920
157e	230822	-121.94200	37.12500	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151921
157f[‡]	230823	-121.94200	37.12500	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151922
157g	230824	-121.94200	37.12500	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151923
157h	230825	-121.94200	37.12500	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151924
157i	230826	-121.94200	37.12500	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151925
157j	230827	-121.94200	37.12500	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151926
157k	230828	-121.94200	37.12500	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151927
157l	230829	-121.94200	37.12500	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151928

Population	**MVZ #**	**Longitude**	**Latitude**	**Locality**	**County**	**Subspecies**	**Major Clade**	**Clade**	**Genbank**
157m	230874	-121.94200	37.11700	Miller cut-off, 0.1 mi E junction Soquel Creek and San Jose Rd.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151929
158*	230859	-122.14028	37.10361	Alba Rd., NE jct Empire Grade	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	*
159*	230862	-122.10611	37.09722	Alba Rd., 2.9 mi E jct Empire Grade	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	*
160*	230856	-122.13778	37.07083	Empire Grade, 1.7 mi N juntion with Felton Empire Rd.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	*
161	230805	-121.75194	37.04611	Summit Rd., 2.9 mi NW Mt. Madonna Rd.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151930
162*	230854	-122.05389	37.04444	Graham Hill Rd., 0.9 mi E junction Zayante Rd.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	*
163*	230844	-121.79250	37.03139	Redwood Rd., 0.9 mi NW junction Hazel Dell Rd.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	*
164a	230812	-121.71667	37.01444	Mt. Madonna Rd., N junction Summit Rd.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151931
164b	230813	-121.71667	37.01444	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151932
164c	230814	-121.71667	37.01444	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151933
164d	230815	-121.71667	37.01444	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151934
164e	230832	-121.71667	37.01444	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151935
164f	230833	-121.71667	37.01444	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151936
164g	230834	-121.71667	37.01444	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151937
164h	230835	-121.71667	37.01444	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151938
164i	230836	-121.71667	37.01444	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151939
164j	230837	-121.71667	37.01444	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151940
165a	226739	-121.67847	37.00379	Hwy. 152 , 5 mi W junction St. Teresa Blvd., vicinity Gilroy	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151941
165b	226740	-121.67847	37.00379	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151942
165c	226741	-121.67847	37.00379	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151943
165d	226742	-121.67847	37.00379	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151944
165e	226743	-121.67847	37.00379	Ibid.	Santa Clara	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151945
166	186613	-122.05676	36.99644	Cave Gulch, W of Empire Grade Rd., near U.C. Santa Cruz	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151946
167*	230846	-122.01056	36.99556	Branciforte Rd., 0.1 mi S jct Glen Canyon Rd.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	*
168	230839	-121.74361	36.99472	Hazel Dell Rd., 0.7 mi W jct Mt. Madonna Rd.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151947
169a	230887	-121.69943	36.99130	Hecker Pass Rd, 2.7 mi SW junction Hwy. 9	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151948
169b	230888	-121.69943	36.99130	Ibid.	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151949
170	181436	-121.71059	36.97927	4.7 mi ENE city limit of Watsonville on Hwy. 152	Santa Cruz	*xanthoptica*	coastal lineage	*xanthoptica* [2]	FJ151950
171[‡]	232660	-121.66700	36.91700	Hwy 129 W of Chittenden Pass, N bank of Pajaro River, Pajaro Valley	Santa Cruz	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151951
172	195674	-121.59588	36.85724	Rocks Rd., 0.5 mi S Hwy. 101	San Benito	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151952

Population	MVZ #	Longitude	Latitude	Locality	County	Subspecies	Major Clade	Clade	Genbank
173	205706	-121.49906	36.80216	San Juan Creek, 3.7 mi S Hwy. 156 at San Juan Bautista	San Benito	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151953
174	211877	-121.89253	36.60021	corner Valenzuela Rd. & Viejo Rd., Monterey	Monterey	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151954
175a	232663	-121.86767	36.58550	Josselyn Canyon Road, 0.85 mi W Hwy. 68	Monterey	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151955
175b	233081	-121.86767	36.58550	Ibid.	Monterey	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151956
176	232661	-121.87500	36.57500	Jct. Aquajto and Monhollan Rds.	Monterey	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151957
177	167462	-121.86131	36.33100	Coast Rd., 7 mi SSE Hwy. 1, S Fork Little Sur River	Monterey	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151958
178	158106	-121.60341	36.10204	Big Creek Reserve, N Section	Monterey	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151959
179	223043	-121.17417	36.08573	20 m S of the 9 mi Marker on San Juan Grade Rd.	Monterey	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151960
180	217508	-120.48024	36.08193	Paluquin Mine near Parkfield, Southernmost Monterey County	Monterey	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151961
181	237493	-121.41194	35.88500	Along Willow Creek Rd, ~4.8 mi E Hwy 1	Monterey	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151962
182	167654	-120.04545	34.79473	San Rafael Mts., Zaca Creek, 1.9 mi W Zaca Lake	Santa Barbara	*eschscholtzii*	coastal lineage	*eschscholtzii*	L75799
183	181460	-116.77583	33.97980	E branch Millard Canyon along Kitching Peak Trail, 6.0 mi NNE Cabazon	Riverside	*eschscholtzii*	coastal lineage	*eschscholtzii*	L75798
184[‡]	237147	-116.63731	32.94351	Wildcat Spring 1.8 mi W Caya Maca Peak, on Boulder Creek Rd	San Diego	*eschscholtzii*	coastal lineage	*eschscholtzii*	FJ151963
185	178729	-116.68000	32.83000	3.5 mi E Alpine on S Access road to I-8 near Willow Rd. Overpass	San Diego	*eschscholtzii*	coastal lineage	*eschscholtzii*	L75800
186	211833	-121.67746	40.52446	0.5 mi ENE Viola on Hwy. 44	Shasta	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151964
187	218069	-121.27800	39.69990	Milsap Bar Rd., 2.2 mi N Bald Rock Rd.	Butte	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151965
188[‡]	173177	-121.01000	39.33000	5 mi N Nevada City on Bald Mt	Nevada	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151966
189	172459	-120.64450	38.90640	15.3 mi E Georgetown on Wentworth Spr. Rd.	El Dorado	*platensis*	clade A	inland lineage (southern *platensis*)	L75813
190[‡]	158006	-120.33700	38.27500	Arnold, N side Upper White Pines Lake	Calaveras	*platensis*	clade A	inland lineage (southern *platensis*)	L75812
191	215830	-121.81090	40.40215	Bluff Springs Station, 1.8 mi S Forward Rd. on Ponderosa Way	Tehama	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151967
192	177876	-120.15226	37.95810	Alder Spring vicinity, 2 mi E Tuolumne	Tuolumne	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151968

Population	MVZ #	Longitude	Latitude	Locality	County	Subspecies	Major Clade	Clade	Genbank
193a	237148	-119.96097	37.93410	Cherry Lake Rd at Crossing of Granite Creek	Tuolomne	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151969
193b	237149	-119.96097	37.93410	Ibid.	Tuolomne	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151970
194	223035	-120.03000	37.92000	Jawbone Ridge	Tuolumne	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151971
195	237150	-119.09975	37.79806	near Hwy 120 W entrance to Yosemite National Park	Mono	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151972
196	157796	-120.18222	37.79528	Wagner Ridge on Cuneo Rd 1.9 mi N Dexter Rd	Tuolomne	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151973
197	223034	-120.15531	37.78531	Wagner Ridge	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151974
198	157798	-120.18389	37.77333	Cuneo Rd ca 200 m W intersection Dexter Rd	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151975
199	157490	-120.13500	37.76528	S slope Wagner Valley on Converse Rd, 0.7 mi N Dexter Rd	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151976
200	157491	-120.11722	37.75472	Converse Rd just S Old Converse Rd, Wagner Valley	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151977
201	237152	-119.76953	37.74303	Hwy 41at Big Meadow lookout, Yosemite National Park	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151978
202	237160	-119.61047	37.73275	1.7 mi from El Capitan parking area, Yosemite National Park	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151979
203[‡]	237157	-119.54278	37.72722	5 m from S side of Vernal Falls along Merced R, Yosemite National Park	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151980
204	237158	-119.53339	37.72692	Vernal Falls & Nevada Falls, Yosemite National Forest	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151981
205a	237161	-119.62575	37.72156	Yosemite Valley N of Cathedral Rocks, Yosemite National Park	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151982
205b	237162	-119.62575	37.72156	Ibid.	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151983
206a	237155	-119.65111	37.71511	Bridalveil Falls, Yosemite National Park	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151984
206b	237156	-119.65111	37.71511	Ibid.	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151985
207a	208445	-119.77364	37.69005	~1.2 mi NE El Portal along Crane Creek, Yosemite National Park	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151986

Population	MVZ #	Longitude	Latitude	Locality	County	Subspecies	Major Clade	Clade	Genbank
207b	237154	-119.76758	37.69303	1.15 mi from Foresta Falls, Crane Creek Watershed, Yosemite NP	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151987
208	237289	-119.68347	37.61364	3.9 mi S on Hwy 41 from Dageer Pass turnoff, Yosemite National Park	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151988
209	237292	-119.65375	37.54031	400 m E of jct of Hwy 41 & S Fork Merced R, Yosemite National Park	Mariposa	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151989
210	169033	-119.63164	37.49503	~15 mi N Oakhurst on Gooseberry Flat Rd.	Madera	*platensis*	clade A	inland lineage (southern *platensis*)	L75816
211	208181	-119.59011	37.40165	Gooseberry Flat, 3.4 mi NE Hwy. 41, near Yosemite Forks	Madera	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151990
212a	244095	-119.62530	37.39610	E side Lewis Fork Creek, S of Deer Run Trail	Madera	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151991
212b	244096	-119.62530	37.39610	Ibid.	Madera	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151992
212c	244097	-119.62770	37.39660	Ibid.	Madera	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151993
212d	244098	-119.62770	37.39660	Ibid.	Madera	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151994
213a	244092	-119.60960	37.38190	Gooseberry Flats Rd., ca. 2 mi NE Hwy. 41	Madera	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151995
213b	244093	-119.61190	37.38050	W side Gooseberry Flats Rd., ca. 2 mi NE Hwy. 41	Madera	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151996
213c	244094	-119.61190	37.38050	Ibid.	Madera	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151997
214	237128	-118.70742	36.77047	Don Cecil Trail, ~2 mi SW Cedar Grove, Kings Canyon National Park	Fresno	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151998
215	237287	-118.98439	36.71394	Mill Creek, ~2 mi NE Pinehurst, Sequoia National Park	Fresno	*platensis*	clade A	inland lineage (southern *platensis*)	FJ151999
216	237130	-118.91317	36.69583	Redwood Camp, ~5 mi SE Grant Grove Village, Kings Cyn National Park	Tulare	*platensis*	clade A	inland lineage (southern *platensis*)	FJ152000
217	169165	-118.95729	36.65472	vicinity Hartland	Tulare	*platensis*	clade A	inland lineage (southern *platensis*)	L75814
218[‡]	237168	-118.89694	36.54611	North side of Yucca Creek near west edge Sequoia National Park	Tulare	*platensis*	clade A	inland lineage (southern *platensis*)	FJ152001
219	237175	-118.87000	36.38222	Along S fork Kaweah River 5.0 mi SE Hwy 198 at Three Rivers	Tulare	*platensis*	clade A	inland lineage (southern *platensis*)	FJ152002
220[‡]	202330	-118.48598	35.04722	Tehachapi Mt. Park, near Campsite #55	Kern	*croceater*	clade A	inland lineage	L75796

Population	MVZ #	Longitude	Latitude	Locality	County	Subspecies	Major Clade	Clade	Genbank
221	195607	-119.02541	34.65289	Alamo-Little Mutau Creek Divide, 2.1-2.4 mi WNW McDonald Peak	Ventura	*croceater*	clade A	inland lineage	L75797
222	185823	-116.92694	34.37222	Crystal Creek above Lucerne Valley, N side San Bernardino Mts.	San Bernardino	*klauberi*	clade A	inland lineage	L75801
223	185844	-116.49009	33.54286	Queen Creek 4.9 mi SE of Hwy. 74 on Santa Rosa Mt. Rd.	Riverside	*klauberi*	clade A	inland lineage	L75803
224a‡	191684	-116.59000	32.99000	Camp Wolahi, Cuyamaca Mts.	San Diego	*klauberi*	clade A	inland lineage	L75804
224b	194908	-116.59000	32.99000	Ibid.	San Diego	*klauberi*	clade A	inland lineage	L75805

1. Statistical support for the monophyly of clade A is low (see text).
2. Tissue provided by Shawn R. Kuchta (no voucher specimens)
3. Tail tips provied by Gary Fellers, Point Reyes National Seashore
4. CAS = California Academy of Sciences accession number

* Sequence excluded from Bayesian analysis because of low quality; also excluded from GenBank

‡ Sequence used in multidivtime analysis