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Uta stansburiana and *Elgaria multicarinata* on the California Channel Islands: Natural Dispersal or Artificial Introduction?

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ABSTRACT.—***Uta stansburiana* and *Elgaria multicarinata* occur on several California Channel Islands, and recent introduction of some populations has been suggested because of similarity in life-history traits and body size to mainland populations. We sequenced representatives of each species from mainland southern California and some of the islands on which they occur. For each species, cytochrome *b* sequence divergence is low across the narrow geographic area sampled. Analyses of 14 haplotypes of *U. stansburiana* suggest long-established residency on Santa Catalina and San Clemente Islands but more recent arrival on San Nicolas and Santa Cruz Islands. Analyses of eight haplotypes of *E. multicarinata* suggest these lizards may have been recently transported to San Nicolas Island.**

The lizards *Uta stansburiana* and *Elgaria multicarinata* are widely distributed in western North America and both occur on some of the Channel Islands off southern California (Stebbins, 1985). It has been assumed that the island populations are naturally occurring (Savage, 1967; Wilcox, 1980; Stebbins, 1985), but this has never been explicitly tested, and recent ecological studies suggest that both lizards were probably introduced on some islands (C. Drost, pers. comm.). Studies of events such as artificial introductions (Jackman, 1998) and dispersal among islands (Thorpe et al., 1994; Brown and Pestano, 1998) have benefited from the inclusion of molecular data. We sequenced a region of cytochrome *b* to evaluate genetic variation among populations of *U. stansburiana* and *E. multicarinata* on the Channel Islands of California and the adjacent mainland.

MATERIALS AND METHODS

Uta stansburiana was collected from Santa Cruz, San Nicolas, Santa Catalina, and San Clemente Islands, and *E. multicarinata* was collected from San Miguel and San Nicolas Islands. Both species were collected from the adjacent mainland (Appendix 1). Lizards were sacrificed by sodium pentobarbital injection and samples of liver and muscle were taken. Voucher specimens were deposited in the collections at the Museum of Vertebrate Zoology, University of California, Berkeley. Tissue samples were stored at –70°C. Additional tissue samples were obtained from the Museum of Vertebrate Zoology Frozen Tissue Collection (Appendix 1).

Genomic DNA was extracted from frozen tissue using standard salt-extraction methods. The primer pair MVZ05 (Smith and Patton, 1991) and cytb2 (Kocher et al., 1989) was used in polymerase chain reactions (PCR) to generate double-stranded product of a fragment of cytochrome *b*. Twenty-two individuals of *U. stansburiana* from 15 populations were sequenced, with fragment lengths of 348–402 base pairs (bp; 20 of 22 samples were the complete 402 bp fragment). Ten individuals of *E. multicarinata* from nine populations were sequenced, yielding fragments with lengths of 340–399 bp (eight of 10 samples were the complete 399 bp fragment). Sequences from this study have been deposited in GenBank under accession numbers AF361497–AF361528 (Appendix 1).

PCR products were purified on Microspin s300 spin-columns (Pharmacia Biotech) and labeled with fluorescent-dye through a cycle-sequencing reaction following standard protocols (Applied Biosystems, Perkin Elmer). Cycle-sequencing products were precipitated with ethanol and magnesium chloride to remove unincorporated dyes, and sequenced using an ABI Prism 377 automated sequencer and associated data collection software (Applied Biosystems). All samples were sequenced and read in both primer directions using Sequence Navigator software (vers. 1.0.1, Applied Biosystems). Sequences were aligned manually using the amino acid translation as a guide. No insertions or deletions were observed within either species, however the region bounded by the primers is one codon (three base pairs) shorter in *E. multicarinata* than in *U. stansburiana*.

Phylogenetic relationships among mtDNA haplotypes were analyzed using PAUP* (vers. 4.0b2a; D. L. Swofford, Sinauer Assoc., Sunderland, MA, 1999). Parsimony analyses were conducted with equal weights for all substitution types, using 10 random addition replicates and TBR branch-swapping. Nonparametric bootstrap analysis with 100 replicates assessed relative support for the parsimony topology (Felsenstein, 1985). Outgroups for parsimony analyses of *U. stansburiana* were samples from New Mexico and Baja California Norte, Mexico (sequences provided by B. Hollingsworth). GenBank sequences of three anguid lizards were used as outgroups for analyses of *E. multicarinata* (*Abronia frosti*, GenBank accession number AF056592; *Gerrhonotus liocephalus*, AF056598; and *Mesaspis gadovii*, AF056600; Chippindale et al., 1998). Minimum-spanning trees (MSTs; Rohlf, 1973) or minimum spanning networks (with more than one equivalent length path among haplotypes; Excoffier and Smouse, 1994) were constructed with Arlequin (vers. 2.0; S. Schneider, D. Roessli, and L. Excoffier, Univ. of Geneva, Switzerland, 2000) using absolute number of pairwise differences between sequences. The haplotype network generated in this manner differs from a phylogenetic tree in that OTUs may be placed as ancestral to other OTUs, a useful consideration for intraspecific analyses (Crandall et al., 1994). Haplotype networks

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TABLE 1. Pairwise genetic divergences among 22 individuals of *Uta stansburiana* from the Channel Islands and mainland of southern California. Identical samples from single localities are grouped together. Above the diagonal are absolute number of substitutions. Below the diagonal are uncorrected percent sequence divergences. Sample numbers and localities as in Appendix 1.

Sample number and locality	1	2	3	4	5, 6, 7	8, 9	10	11	12	13	14	15	16	17	18	19, 20, 21	22
1 Santa Barbara Co.	–	2	2	1	3	3	2	3	3	3	8	9	7	12	11	11	10
2 Santa Barbara Co.	0.5	–	0	1	3	3	2	3	3	3	8	9	6	12	11	11	10
3 Santa Cruz Isl.		0	–	1	3	3	2	3	3	3	8	9	6	12	11	11	10
4 Ventura Co.	0.2	0.2	0.2	–	2	2	1	2	2	2	7	8	6	11	10	10	9
5, 6, 7 Ventura Co.	0.7	0.7	0.7	0.5	–	0	1	2	2	2	7	8	6	11	10	10	9
8, 9 San Nicolas Isl.	0.7	0.7	0.7	0.5	0	–	1	2	2	2	7	8	6	11	10	10	9
10 Los Angeles Co.	0.5	0.5	0.5	0.2	0.2	0.2	–	1	1	1	6	7	5	10	9	9	8
11 Los Angeles Co.	0.7	0.7	0.7	0.5	0.5	0.5	0.2	–	2	2	7	8	6	11	10	10	9
12 Los Angeles Co.	0.7	0.7	0.7	0.5	0.5	0.5	0.2	0.5	–	2	7	8	6	11	10	10	9
13 Los Angeles Co.	0.7	0.7	0.7	0.5	0.5	0.5	0.2	0.5	0.5	–	7	8	6	11	10	10	9
14 Orange Co.	2	2	2	1.7	1.7	1.7	1.5	1.7	1.7	1.7	–	1	1	8	7	7	6
15 Orange Co.	2.2	2.2	2.2	2	2	2	1.7	2	2	2	0.2	–	2	9	8	8	7
16 San Diego Co.	2	1.7	1.7	1.7	1.7	1.7	1.4	1.7	1.7	1.7	0.3	0.6	–	6	6	6	7
17 Santa Catalina Isl.	3	3	3	2.7	2.7	2.7	2.5	2.7	2.7	2.7	2	2.3	1.7	–	1	1	1
18 Santa Catalina Isl.	2.7	2.7	2.7	2.5	2.5	2.5	2.2	2.5	2.5	2.5	1.7	2	1.7	0.2	–	0	1
19, 20, 21 San Clemente Isl.	2.7	2.7	2.7	2.5	2.5	2.5	2.2	2.5	2.5	2.5	1.7	2	1.7	0.2	0	–	1
22 San Clemente Isl.	2.9	2.9	2.9	2.6	2.6	2.6	2.3	2.6	2.6	2.6	1.7	2	2.1	0.3	0.3	0.3	–

were superimposed on a map of the study area. Combining these two methods (parsimony and MST construction) allows examination of the data under different assumptions.

RESULTS

Among the samples of *U. stansburiana*, uncorrected percent sequence divergence ranged from 0–3% (zero to 12 substitution differences; Table 1) and the transition:-transversion ratio, estimated using maximum likelihood, was 1.5:1. Twelve of 21 variable nucleotide positions were parsimony informative among the ingroup samples. Several samples had identical sequences (Table 1). Parsimony analysis of the 14 unique haplotypes of *U. stansburiana* and three outgroups yielded 18 most parsimonious trees (MPTs; strict consensus shown in Fig. 1A). Including outgroup taxa, tree length was 78 steps, and the consistency index (CI) was 0.859. Considering only ingroup taxa, tree length was 22 steps, and the CI was 0.955. The base of the tree was an unresolved polytomy of three groups. All haplotypes from Santa Catalina and San Clemente Islands formed a group with strong bootstrap support (97%). Also well supported (95% bootstrap support) was a group of samples from the northern part of the mainland study area plus San Nicolas and Santa Cruz Islands. Relationships within this group were unresolved. The third group in the phylogeny had relatively low bootstrap support (67%) and consisted of southernmost mainland samples (Orange and San Diego Counties).

Among the samples of *E. multicarinata*, uncorrected percent divergence ranged from 0–4% (zero to 16 substitution differences; Table 2) and the transition: transversion ratio was 2.1:1. Of 18 variable nucleotide positions, 14 were parsimony informative (excluding outgroup taxa). As with *U. stansburiana*, some samples of *E. multicarinata* had identical sequences (Table 2). Parsimony analysis of eight unique haplotypes of *E. multicarinata* and three outgroups yielded a single MPT (Fig. 1B). Including outgroups, tree length was 151 steps, and CI was 0.767. Considering only ingroup taxa, tree length was 21 steps, and CI was 0.950. The tree had a basal divergence between two moderately well-supported groups. Haplotypes from San Nicolas and San Miguel Islands clustered with mainland samples from Ventura and Kern Counties. Bootstrap support for this group was 83%. Samples from San Diego, Orange, and Los Angeles Counties formed a separate group with 86% bootstrap support.

The minimum-spanning trees (MSTs) for both species recovered the same groups as parsimony analyses, but placed haplotypes in ancestor-descendent relationships, whereas parsimony joined closely related haplotypes as sister taxa. The network for *U. stansburiana* showed two distinct patterns of divergence for samples from the Channel Islands (Fig. 2A). The Santa Catalina/San Clemente Islands group of populations (samples 17–22) was relatively divergent (six substitutions) from its closest mainland relative (sample 16). In contrast, samples from San Nicolas Island (samples 8 and 9) were identical to mainland Ventura County samples (samples 5–7, Point Mugu Naval Air Station). *Uta stansburiana* from Santa Cruz Island (sample 3) was also identical to a mainland sample (sample 2). The pattern seen in *E. multicarinata* was similar to the second pattern observed for *U. stansburiana* (Fig. 2B). The sample of *E. multicarinata* from San Miguel Island (sample 3) was identical to one haplotype from San Nicolas Island (sample 4), and these samples differed by two substitutions from the second San Nicolas sample (sample 5). The island samples of *E. multicarinata* differed by 1 to 3 substitutions from a mainland sample at Point Mugu, Ventura County (sample 2).

DISCUSSION

Low sequence divergences recovered for both *U. stansburiana* and *E. multicarinata* are similar to values

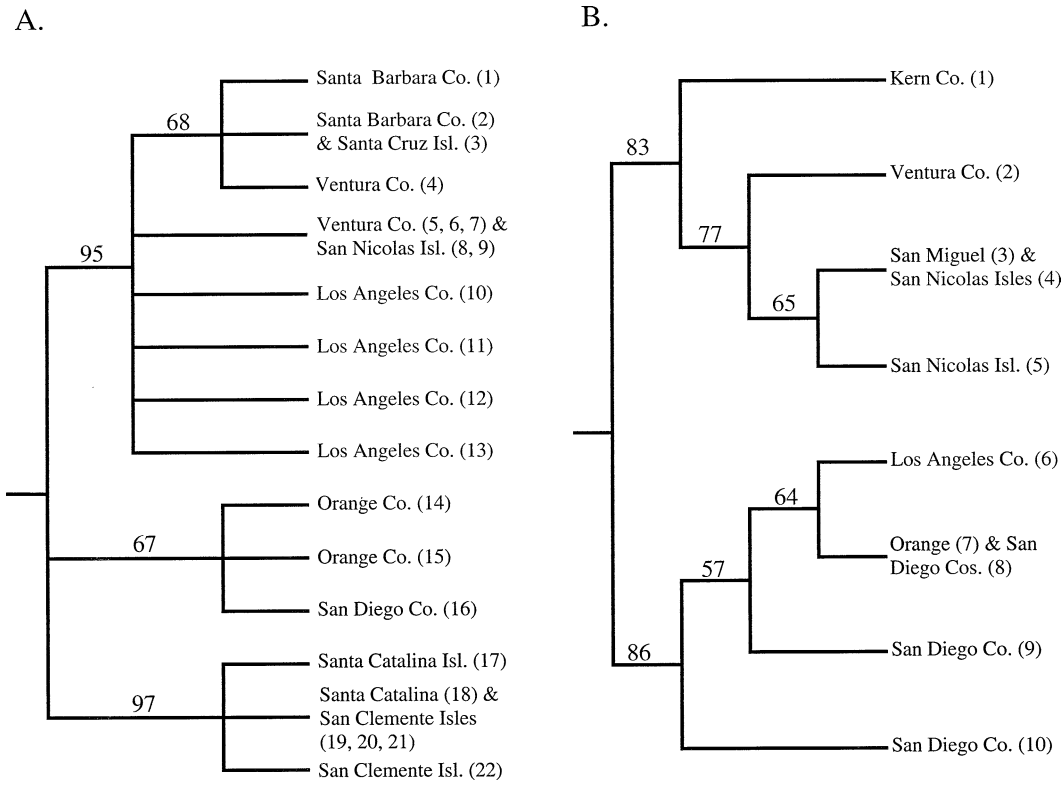

FIG. 1. Results of parsimony analyses. Identical sequences treated as single OTUs. Numbers on branches are bootstrap values greater than 50% (from 100 replicates). Lengths and consistency indices (CI) exclude outgroup taxa. (A) *Uta stansburiana*, strict consensus of 18 MPTs, length 22, CI 0.955. (B) *Elgaria multicarinata*, single MPT, length 21, CI 0.950.

recovered in other intraspecific comparisons over restricted geographic ranges (Upton and Murphy, 1997; Orange et al., 1999). The small number of variable positions results in low bootstrap support for parsimony topologies. Despite low variation overall, some populations of *U. stansburiana* had more than one haplotype (Table 1, Fig. 2A), and the samples of *E. multicarinata* from San Nicolas Island were not identical (Table 2, Fig. 2B).

Uta stansburiana on Santa Catalina and San Clemente has diverged in life-history characteristics (annual instead of multi-annual reproductive cycle) and morphology (larger body size) from mainland populations (W. Mautz, pers. comm.). The mtDNA divergence

TABLE 2. Pairwise genetic divergences among 10 individuals of *Elgaria multicarinata* from Channel Islands and mainland of southern California. Above the diagonal are absolute number of substitutions. Below the diagonal are uncorrected percent sequence divergences. Sample numbers and localities as in Appendix 1.

Sample number and locality	1	2	3	4	5	6	7	8	9	10
1 Kern Co.	–	3	4	4	4	10	10	10	10	8
2 Ventura Co.	0.9	–	1	1	3	12	13	12	12	11
3 San Miguel Isl.	1.2	0.3	–	0	2	13	14	13	13	12
4 San Nicolas Isl.	1.2	0.3	0	–	2	13	14	13	13	12
5 San Nicolas Isl.	1.2	0.8	0.5	0.5	–	15	16	15	15	14
6 Los Angeles Co.	3	3	3.3	3.3	3.8	–	1	4	4	5
7 Orange Co.	3	3.3	3.5	3.5	4	0.3	–	0	3	4
8 San Diego Co.	3	3.3	3.5	3.5	4	0.3	0	–	3	4
9 San Diego Co.	3	3.1	3.4	3.4	3.9	1	0.8	0.8	–	5
10 San Diego Co.	2.4	2.8	3	3	3.5	1.3	1	1	1.3	–

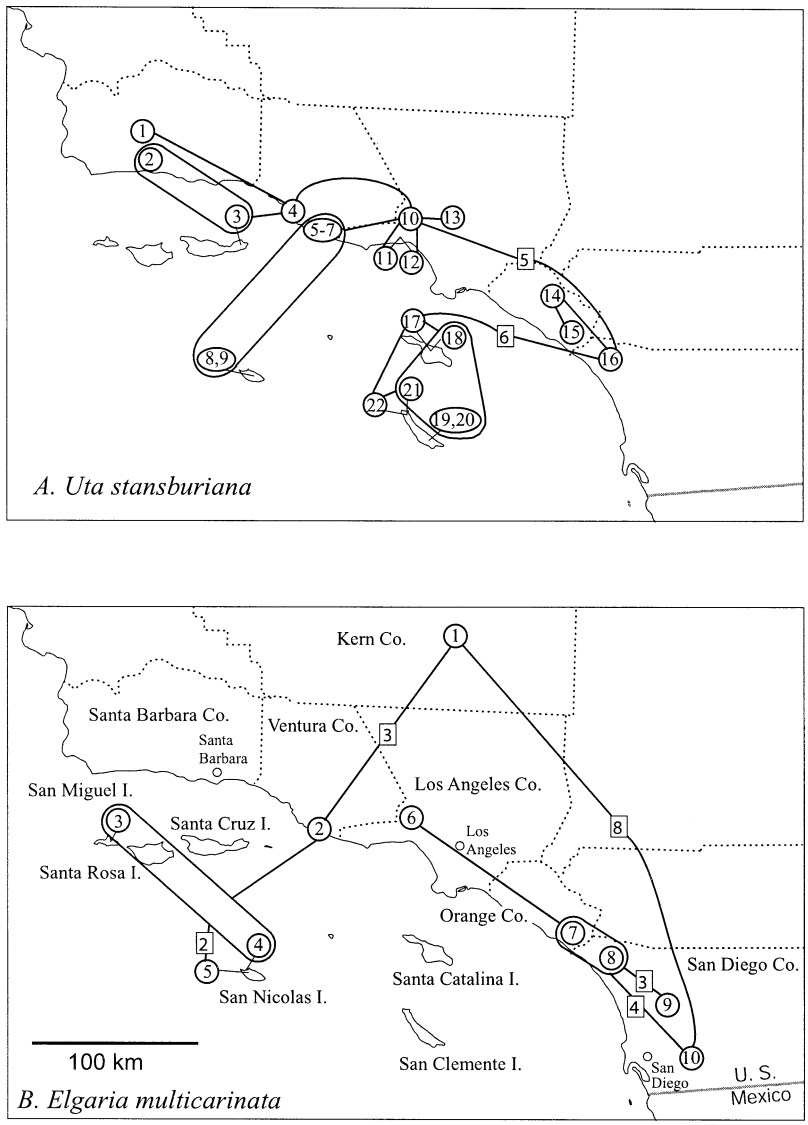

FIG. 2. Minimum-spanning trees superimposed on a map of the study area. Numbers within circles correspond to samples listed in Tables 1 and 2. Identical haplotypes are grouped, lines between haplotypes and groups indicate a single substitution, and numbers in squares indicate the number of substitutions between haplotypes when greater than one. For clarity, fine lines connect some sample numbers to localities. (A) *Uta stansburiana*. (B) *Elgaria multicarinata*.

between the island samples and the most similar mainland sample (6–7 bp, 1.7–2.1%) is the largest genetic break that we found within *U. stansburiana*. The ecological and genetic differences suggest long-established populations of *U. stansburiana* on Santa Catalina and San Clemente Islands. Genetic identity and near-identity (Table 1) of samples from Santa Catalina and San Clemente may be because of regular exchange of genetic material between the islands, or one of the islands may have been colonized from the other. The islands are 34 km apart, and natural rafting between islands is plausible, although perhaps unlikely on a regular basis. Anthropogenic transfer of *U. stansburiana* between Santa Catalina and San Clemente Islands is also possible.

Uta stansburiana on San Nicolas Island is genetically identical to mainland samples from Point Mugu Naval Air Station. Both sites are U.S. Navy installations, and there is regular transport of cargo between them by boat and aircraft (G. Smith, pers. comm.). Historical records for *U. stansburiana* on San Nicolas Island are nonexistent, and as recently as 1980 the species was not included on a list of reptiles occurring there (Wilcox, 1980). Genetic data from our study suggest recent

colonization and inadvertent transport in naval shipments as a plausible mechanism. Recent, natural colonization of San Nicolas Island from Point Mugu is less likely, given distance (98 km) and unfavorable ocean currents (Jones, 1971).

Uta stansburiana from Santa Cruz Island is identical to a mainland sample from near Santa Barbara. Parts of Santa Cruz Island have been used as a sheep ranch since 1830, during which time there have been regular and frequent boat trips from mainland Santa Barbara County, as well as occasional landings by light aircraft and helicopter (T. Coonan, pers. comm.). In the mid-1800s, when ranching was being established, considerable amounts of fencing and building material were moved out to the island. Lizards could easily have been inadvertently transported to the island with these supplies or during any subsequent movements of cargo. Alternatively, lizard colonization may have occurred naturally. Santa Cruz Island is relatively close to the mainland (30 km; Wilcox, 1980), and rafting from the mainland has been proposed as the means by which reptiles and amphibians colonized the Channel Islands (Savage, 1967; Yanev, 1980). Under either scenario, natural rafting or human-mediated, the genetic data support recent movement of *U. stansburiana* to the island.

Samples of *E. multicarinata* from San Nicolas Island are also genetically most similar, although not identical, to lizards from Point Mugu. Only relatively recent collections have reported *E. multicarinata* on San Nicolas Island (Banta and Wilson, 1976), and the distribution of *E. multicarinata* on the island suggests recent introduction. Lizards are found only on the southeast third of the island, where the Navy barge landing is located, even though there is suitable, contiguous, unoccupied habitat over most of the island. In addition, *E. multicarinata* has been expanding its range on the island since at least 1985 (C. Drost and T. Murphey, pers. comm.).

Late Pleistocene fossils of *E. multicarinata* are known from San Miguel Island (Guthrie, 1993), and the island may have remained above water over the last 500,000 years (Vedder and Howell, 1980). The U.S. Navy has managed both San Nicolas and San Miguel Islands for more than 50 years, during which time there have been regular helicopter flights from Point Mugu and between the two islands. If *E. multicarinata* has persisted on San Miguel Island since the Pleistocene, recent arrival on San Nicolas Island could be the result of transport either from San Miguel Island or the mainland. Genetic identity of the sample from San Miguel and one of the samples from San Nicolas Islands suggests movement between islands.

Our sampling of *E. multicarinata* is not as extensive as for *U. stansburiana*. Increased sampling of *E. multicarinata* on the mainland is likely to reveal additional mtDNA haplotypes and provide a test of whether island-dwelling *E. multicarinata* result from multiple dispersal events. This possibility is suggested by the genetic variability recovered in this study. The presence of *U. stansburiana* on the Channel Islands did result from multiple movements at different points in time. The genetic divergence between Santa Catalina/San Clemente Island and mainland populations parallels differences in life history and body size, suggesting long-term residency on those islands. This contrasts with the genetic identity and similar body size and reproductive cycle of San Nicolas Island and mainland lizards, all of which suggest recent colonization.

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APPENDIX 1

Uta stansburiana and *Elgaria multicarinata* samples from Channel Islands and adjacent mainland of southern California. For each individual sequenced, information is presented as sample number, county, island (if applicable), catalog or collector number, and GenBank accession number. Abbreviations: GB, GenBank; MVZ, Museum of Vertebrate Zoology; RF, R. Fisher field series.

Uta stansburiana. Sample 1, Santa Barbara Co., MVZ 137510, GB AF361517. Sample 2, Santa Barbara Co., MVZ 229985, GB AF361502. Sample 3, Santa Barbara Co., Santa Cruz Island, MVZ 230913, GB AF361506. Sample 4, Ventura Co., MVZ 230916, AF361513. Sample 5, Ventura Co., MVZ 229986, GB AF361503. Sample 6, Ventura Co., MVZ 229987, GB AF361504. Sample 7, Ventura Co., MVZ 229988, GB AF361505. Sample 8, Ventura Co., San Nicolas Island, MVZ 230910, GB AF361516. Sample 9, Ventura Co., San Nicolas Island, MVZ 230911, GB AF361497. Sample 10, Los Angeles Co., MVZ 229978, GB AF361512. Sample 11, Los Angeles Co., MVZ 229979, GB AF361511. Sample 12, Los Angeles Co., MVZ 229980, GB AF361500. Sample 13, Los Angeles Co., MVZ 229977, GB AF361501. Sample 14, Orange Co., RF 2.1.A, GB AF361508. Sample 15, Orange Co., RF 102B, GB AF361507. Sample 16, San Diego Co., MVZ 150120, GB AF361518. Sample 17, Los Angeles Co., Santa Catalina Island, MVZ 230915, GB AF361515. Sample 18, Los Angeles Co., Santa Catalina Island, MVZ 230914, GB AF361514. Sample 19, Los Angeles Co., San Clemente Island, MVZ 229983, GB AF361498. Sample 20, Los Angeles Co., San Clemente Island, MVZ 229984, GB AF361499. Sample 21, Los Angeles Co., San Clemente Island, MVZ 229981, GB AF361509. Sample 22, Los Angeles Co., San Clemente Island, MVZ 229982, GB AF361510.

Elgaria multicarinata. Sample 1, Kern Co., MVZ 137826, GB AF361519. Sample 2, Ventura Co., MVZ 229976, GB AF361520. Sample 3, Santa Barbara Co., San Miguel Island, MVZ 230920, GB AF361521. Sample 4, Ventura Co., San Nicolas Island, MVZ 230921, GB AF361522. Sample 5, Ventura Co., San Nicolas Island, MVZ 230922, GB AF361523. Sample 6, Los Angeles Co., MVZ 229972, GB AF361524. Sample 7, Orange Co., R. Fisher, GB AF361525. Sample 8, San Diego Co., MVZ 230917, GB AF361526. Sample 9, San Diego Co., MVZ 229974, GB AF361527. Sample 10, San Diego Co., MVZ 230919, GB AF361528.