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Phylogeographic Origin of California Slender Salamanders (*Batrachoseps attenuatus*) in the Sutter Buttes

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ABSTRACT.—**The phylogeny of California Slender Salamanders (*Batrachoseps attenuatus*), which inhabits Northern California's Coast Ranges and Sierra Nevada foothills, was previously investigated by Martínez-Solano et al. (2007), who recovered a monophyletic species that contained five geographically cohesive major clades. However, a population isolate of *B. attenuatus* found in the Sutter Buttes, a geographically isolated volcanic mountain range within the Sacramento Valley, was not available in their phylogenetic analysis. We sequenced the ~780-base pair segment of the mitochondrial DNA cytochrome b (cytb) gene used in Martínez-Solano et al. (2007) to examine the phylogenetic placement of this isolated population within the *B. attenuatus* complex. Our results, based on a single mitochondrial marker, indicate that the Sutter Buttes population of *B. attenuatus* is genetically distinct and falls within the Martínez-Solano et al. (2007) "East Bay/Sierra subclade" that, in turn, is nested within their "Eastern" major clade. Although we cannot accurately estimate how long the Sutter Buttes population has been isolated, *B. attenuatus* was likely able to colonize the Sutter Buttes during pluvial Pleistocene interglacials when more contiguous woodlands may have opened dispersal corridors across the Great Central Valley.**

RESUMEN.—**La filogenia de Salmandras Delgadas de California (*Batrachoseps attenuatus*), que habitan las cordilleras costeras del norte de California y las estribaciones de la Sierra Nevada, fue investigada previamente por Martínez-Solano y otros (2007) quienes recuperaron una especie monofilética que contenía cinco clados principales que eran geográficamente cohesivos. Sin embargo, una población aislada de *B. attenuatus* que vive en los Sutter Buttes, una cadena montañosa volcánica geográficamente aislada dentro del Valle de Sacramento, no estaba disponible en su análisis filogénico. Secuenciamos ~780 segmentos de pares de bases del gen de ADNmt citocromo b (cytb) utilizado en Martínez-Solano y otros (2007) para examinar la colocación filogénica de esta población aislada dentro del complejo *B. attenuatus*. Nuestros resultados, basados en un solo marcador mitocondrial, indican que la población de Sutter Buttes de *B. attenuatus* es genéticamente distintiva y se encuentra dentro de la categoría de Martínez-Solano y otros (2007) "East Bay/Sierra subclade" que a su vez está anidado dentro de su clado mayor "oriental." Aunque no podemos estimar con precisión cuánto tiempo ha estado aislada la población de los Sutter Buttes, es probable que *B. attenuatus* haya podido colonizar los Sutter Buttes durante el pluvial de los interglaciares del Pleistoceno cuando los bosques más contiguos pueden haber abierto corredores de dispersión a través del Gran Valle Central.**

The dynamic geological history and resulting diverse topography of California have produced a unique and complex reptile and amphibian species assemblage that is second only to Texas in terms of U.S. species richness (Peabody and Savage, 1958; Stebbins, 2003; Stebbins and McGinnis, 2012; Thomson et al., 2016). A biogeographic pattern observed across several members of California's herpetofauna is occupation of the Coast Ranges and Sierra Nevada foothills, but not the intervening Great Central Valley (Stebbins, 2003; Stebbins and McGinnis, 2012). The California Slender Salamanders (*Batrachoseps attenuatus*) follows this pattern, although unlike other co-distributed plethodontid species (Yellow-eyed Ensatinas [*Ensatina eschscholtzii xanthoptica*], Arboreal Salamanders [*Aneides lugubris*]), some isolated populations of *B. attenuatus* do occur within the Great Central Valley (Hayes and Cliff, 1982; Stebbins, 2003; Stebbins and McGinnis, 2012). One such population of *B. attenuatus* was discovered by Dr. Thomas L. Rodgers in 1942 at the Sutter Buttes, an enigmatic mountain range of volcanic origin that erupted near the center of the Sacramento Valley, in the northern Great Central Valley. This population is geographically isolated from other highland regions by the surrounding valley floor, which is currently inhospitable habitat for *Batrachoseps* (Fig. 1) (Stebbins, 2003; Anderson, 2004). Unlike other regions of California where the species can often be abundant (Cope, 1883; Hubbard, 1903; Storer, 1925), Slender Salamanders at the Sutter Buttes are uncommonly encountered even during focused surveys (Anderson, 2004). During an inventory of herpetofauna at the Sutter Buttes, where drift-fences were used in conjunction with pitfall traps, only a single *B. attenuatus* was captured over a combined 336 trap nights during the presumably optimal rainy season (March and April) (Olson, 2007). Whether *B. attenuatus* is rare, elusive, or a combination of both at the Sutter Buttes is unknown, but its apparent rarity does raise the possibility that it may pose a conservation concern in the region.

The phylogenetics of *Batrachoseps* has been studied throughout California, with many morphologically similar but genetically diverse species lineages identified over the past several decades (Marlow et al., 1979; Jockusch et al., 1998; Wake, 2006). The role of geographic isolation and resulting speciation within *Batrachoseps* is clear throughout Central and Southern California, with isolation from tectonic activity being a primary mechanism for lineage diversification (Jockusch et al., 2001; Jockusch and Wake, 2002; Wake, 2006). The phylogeography of *B. attenuatus* and the role of the Great Central Valley as an isolating mechanism has also been examined, with currently disjunct Coast Ranges and Sierra Nevada foothill populations showing a historical connection through the "Trans-Valley Leak" (Peabody and Savage, 1958; Martínez-Solano et al., 2007). This leak, from the San Francisco Bay Area east to the Sierra Nevada across the Great Central Valley, has also been

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identified in other plethodontid salamanders (*A. lugubris* [Reilly et al., 2015] and *E. e. xanthoptica* [Kuchta et al., 2009]), and potentially occurs in several reptiles (Ring-necked Snakes [*Diadophis punctatus*] [Fontanella et al., 2008], Sharp-tailed Snakes [*Contia tenuis*] [Feldman and Hoyer, 2010], and California Mountain Kingsnakes [*Lampropeltis zonata*] [Myers et al., 2013]).

Although Martínez-Solano et al. (2007) documented the historical leak of *B. attenuatus* across the Great Central Valley followed by an inferred northward expansion along the Sierra Nevada foothills, their study did not include the isolated population occupying the Sutter Buttes. In 2007, EOO was able to conduct fieldwork and acquire *B. attenuatus* genetic material for the first time from the Sutter Buttes. We use these samples to examine three hypotheses for the origins of the currently isolated Sutter Buttes population: (1) a natural westward dispersal from the Sierra Nevada foothills to the Sutter Buttes, (2) a natural eastward dispersal from the northern Coast Ranges to the Sutter Buttes, and (3) a much more recent human-mediated introduction in historic times.

Materials and Methods

We examined *B. attenuatus* tissue samples collected during a broader inventory study of the herpetofauna of the Sutter Buttes in 2007 (Olson et al., 2016). Following the same protocols for tissue collection used in Olson et al. (2016), we collected additional samples from Marin and Placer counties in 2018 to add potentially informative samples for placing Sutter Buttes samples within the Martínez-Solano et al. (2007) phylogeny (Supplementary Material).

mtDNA Phylogenetics.—We extracted DNA from tail tip tissue samples by using a standard salt extraction protocol (Sambrook and Russell, 2001). An ~780-base pair segment of the mitochondrial DNA (mtDNA) cytochrome b (cytb) gene was amplified using standard molecular techniques (primers: MVZ15 and MVZ16; Mortiz et al., 1992), and templates were cleaned with EXOSAP-IT (Thermo Fisher Scientific, USA) and sequenced (Genewiz, USA). All sequences are deposited in GenBank (accession nos. MN37832–MN378336). We also downloaded a data set of cytb sequence data generated by Martínez-Solano et al. (2007) that included all individuals of their Eastern clade (the most likely closest relatives to the Sutter Buttes *B. attenuatus* based on geographic proximity) and sparser sampling from all other clades, making sure to include representatives of each minor clade/subclade within the four additional larger clades identified by Martínez-Solano et al. (2007) and data for the outgroup taxon, Black-bellied Slender Salamanders (*B. nigriventris*). We obtained our preferred phylogenetic tree under likelihood (RAxML-HPC v8.2.12; Stamatakis, 2014) on the CIPRES science gateway (Miller et al., 2010) by using the GTR+Γ substitution model, and bootstrapping was halted automatically using the autoMRE criteria. Martínez-Solano et al. (2007) used a structured sampling design in which all individuals were sequenced for cytb, and subsets of those samples were also sequenced for three additional mtDNA fragments: 16s, cox1, and nad4. However, this subsampling included only one sample from the Sierra Nevada foothills, which was found to be sister to three haplotypes from Napa County, California, in all four mtDNA fragments (Supplementary Material). We only sequenced cytb for our new samples given that our preliminary analyses showed all four mtDNA fragments provided the same placement for the single individual Martínez-Solano et al. (2007) sequenced from the Sierra Nevada foothills and that cytb was by far the most variable and informative marker in their study with multiple representatives from the Sierra Nevada foothills. Martínez-Solano et al. (2007) sampled even fewer individuals for the nuclear DNA gene fragment (RAG-1) and did not include any samples from the Sierra Nevada foothills. Our preliminary analyses of downloaded RAG 1 sequences found it to be uninformative for the Sierra/East Bay clade (Supplementary Material; a hard polytomy of largely identical sequences); given these results, we restricted our sequencing of new material to cytb.

To further clarify the relationship of Sutter Buttes *B. attenuatus*, we also generated a haplotype network in R (R Core Team, 2018) by using the ape package (Paradis et al., 2004) for reading DNA sequence data and the pegas package (Paradis, 2010) to reconstruct the network.

Results

We sequenced cytb for 10 *B. attenuatus* individuals sampled from three locations within the Sutter Buttes plus two additional specimens from the Sierra Nevada foothills in Placer County and four from more coastal Marin County (Fig. 2). Our phylogeny recovered all of the major clades discovered in Martínez-Solano et al. (2007) with reasonable bootstrap support (>70%), with the exception of the "southern_north" clade (bootstrap = 52%) but low support for their interrelationships (Fig. 3). This lack of resolution for interclade relationships differs slightly from Martínez-Solano et al. (2007), presumably because their interclade relationships were inferred using a larger mitochondrial data set (Supplementary Material).

We found that the three cytb haplotypes that comprise the Sutter Buttes together form a unique, strongly differentiated clade (bootstrap = 95%) that is roughly equally divergent from lineages from the Sierra Nevada foothills and a single sampling site (MS_59) from the Martínez-Solano et al. (2007) East Bay clade (Figs. 2, 3). The well-supported branch leading to the Sutter Buttes subclade demonstrates that this clade is evolutionarily distinct and not a result of a recent human-mediated introduction.

Discussion

Sutter Buttes Population Phylogeny.—Our maximum likelihood phylogeny and haplotype network demonstrate two key results for the Sutter Buttes *B. attenuatus*. First, they constitute a distinct, evolutionarily unique group that is not derived from a human-mediated dispersal event. It is always possible that they are the result of human movement, such as through the transport of soil as shown in Martínez-Solano and Lawson (2009) for the species, and that previous research failed to sample the entire clade from which the Sutter Buttes animals are derived, but we have no evidence suggesting that this is the case. The Martínez-Solano et al. (2007) sampling, augmented by our new samples from the Sierra and Bay Area, is geographically quite complete, and we feel confident that the isolated Sutter Buttes *B. attenuatus* are not a result of a recent, human-mediated introduction, especially given the relatively long branch leading to individuals in the Sutter Buttes (Fig. 3). Based on this, we reject hypothesis 3 (human-mediated introduction in historic times).

Differentiating between hypothesis 1 (ancestral movement from the Sierra Nevada foothills west to the Sutter Buttes) and hypothesis 2 (ancestral movement from the inner coast range east) is more subtle. All inner coast range members of the

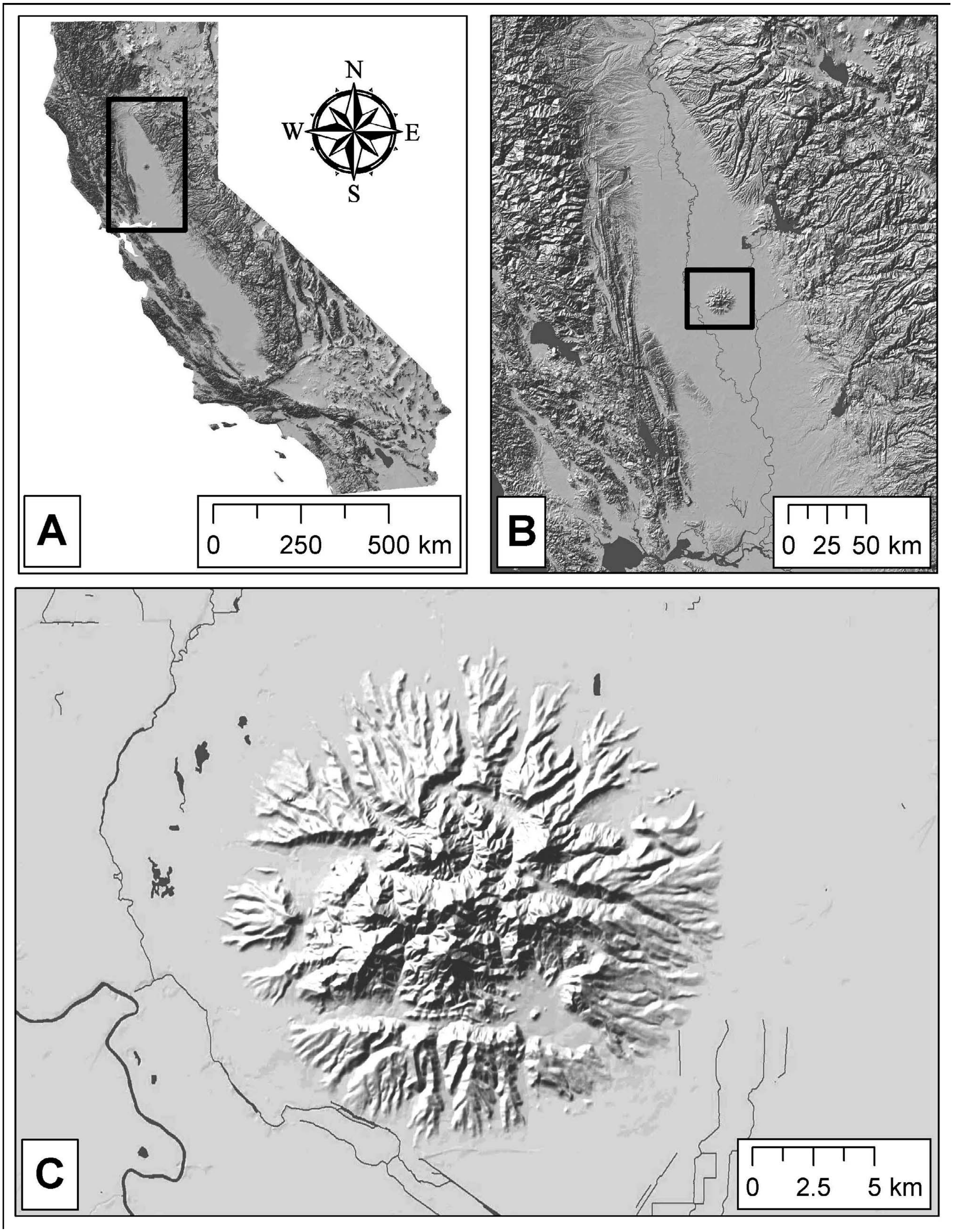

FIG. 1. (A) Topography of California. (B) Topographic detail of the Sacramento Valley with Sutter Buttes highlighted. (C) Further detail of the Sutter Buttes and surrounding lowlands.

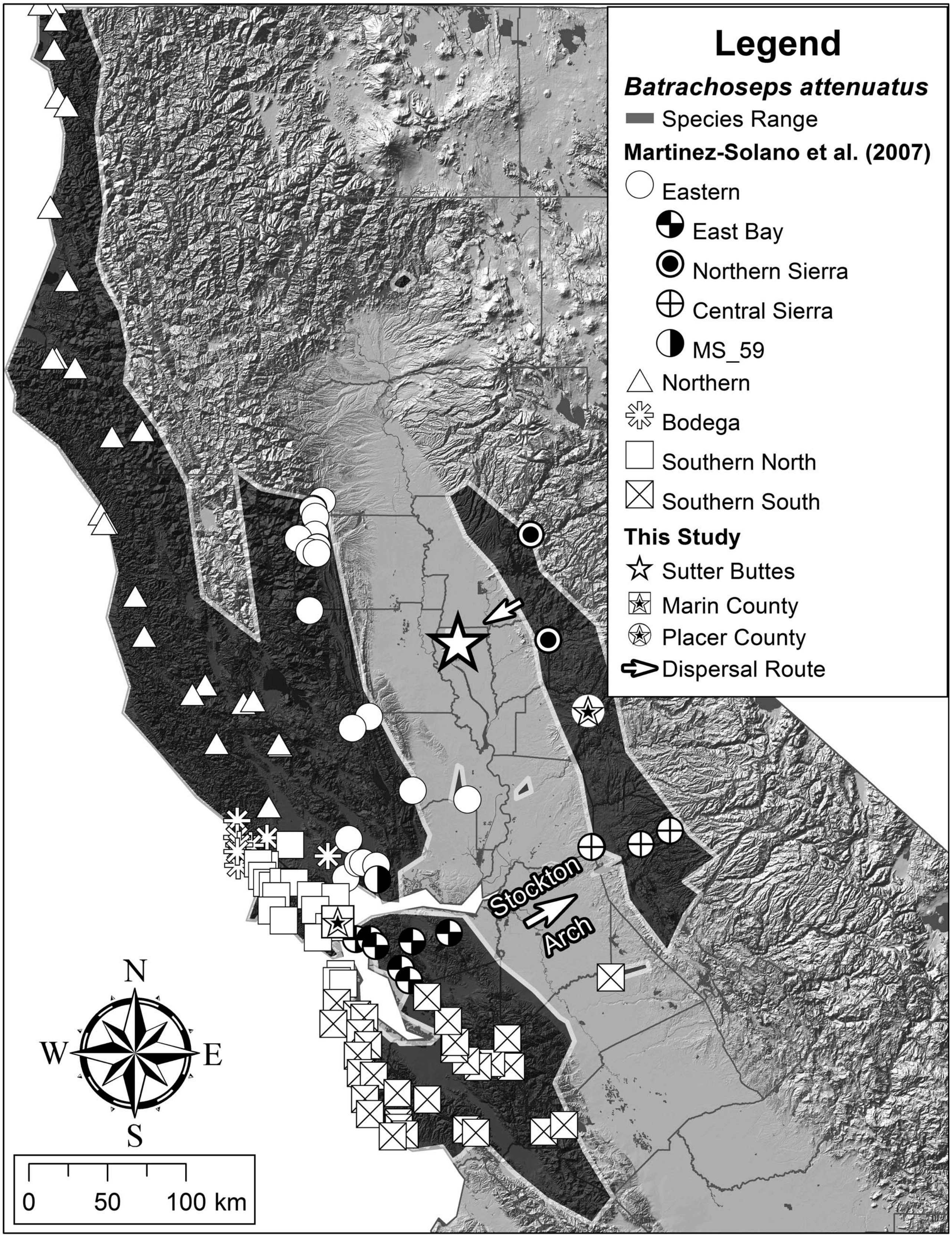

FIG. 2. Map of *B. attenuatus* range within California derived from University of California, Berkeley Museum of Vertebrate Zoology records. Sampling locations and population assignments are from Martínez-Solano et al. (2007), with additional samples and the hypothesized two-stage dispersal routes also shown (white arrows).

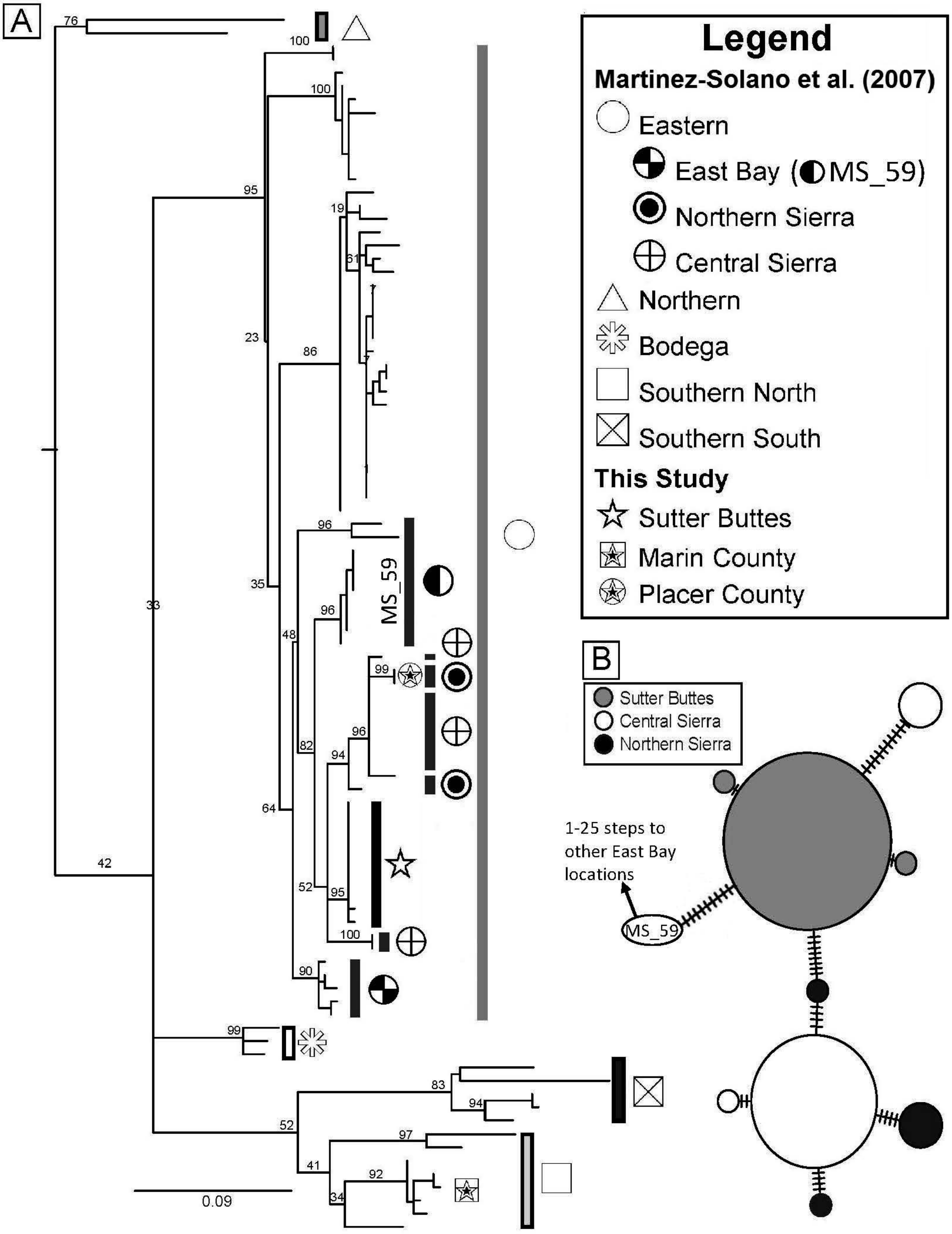

FIG. 3. (A) Maximum likelihood phylogeny of the mtDNA cytb gene for *B. attenuatus* with bootstrap support for major clades indicated at each node. The phylogeny includes all individuals of the "Eastern" clade from Martínez-Solano et al. (2007), limited sampling from the other major clades of that paper, and all new samples included here. (B) mtDNA cytb haplotype network for *B. attenuatus* from the Sutter Buttes, Sierra Nevada foothills and East Bay clades. The phylogeny was rooted with an individual of *B. nigriventris* (DBW6459; EU011253.1), which was removed for the phylogeny for visual clarity.

Eastern clade (Fig. 2, white circles), including those in closest geographic proximity to the Sutter Buttes, form a monophyletic group (bootstrap = 86%) to the exclusion of the Sutter Buttes Salamanders (Fig. 3), providing evidence against hypothesis 2. However, the evidence in support of a Trans-Valley Leak followed by a second migration westward from the Northern or Central Sierra clades, versus a single eastern and northern expansion from the East Bay (and in particular, populations at or near MS_59) that populated the Sierra foothills and the Sutter Buttes simultaneously, is equivocal at best and relies on weak nodal support (bootstrap = 52%; Fig. 3) from a single mitochondrial gene. Given that weak support, the geographical proximity of the Sierran populations to the east, and similar observations of isolated Sutter Buttes populations being most closely related to their disjunct populations to the east (Common Sagebrush Lizards [*Sceloporus graciosus*] [Boyd, 1996]; mygalomorph spiders [Leavitt et al., 2015]), we tend to favor the two-step model and discuss it further below. However, more data with greater resolving power are clearly needed to fully answer this question.

Paleogeological Context of the Sutter Buttes.—The Sutter Buttes were formed through volcanic activity occurring between 1.59 and 1.3 million years ago (mya) (Williams, 1929; Williams and Curtis, 1977; Hausback et al., 1990; Hausback and Nilsen, 1999). At the time of formation, the Sacramento Valley in the proximity of the Sutter Buttes was a fluvial plain, with deposits of the Laguna Formation lying atop what is known as the "Sutter formation", a conglomeration of various alluvial deposits (Springhorn, 2008). At this time, the Sacramento River is thought to have drained into a lacustrine environment in the San Joaquin basin (Harden, 1998). Beginning ∼1.4–1.2 mya, the drainage of the Great Central Valley to the Pacific Ocean was cut off by tectonic activity of the rising Coast Ranges (Harden, 1998; Sarna-Wojcicki, pers. comm.). This resulted in the creation of a large lake spanning the Great Central Valley known alternatively as "Lake Clyde" or "Corcoran Lake" (Bartow, 1991; Sarna-Wojcicki, 1995; Harden, 1998). Lake Clyde persisted until the opening of the Carquinez Straits ∼660,000–634,000 ya, thus forming the drainage system of the Sacramento and San Joaquin Valleys as they exist today (Sarna-Wojcicki et al., 1985; Sarna-Wojcicki, 1995). The area surrounding the Sutter Buttes then returned to a fluvial deposition basin of the Sacramento and Feather rivers (Springhorn, 2008).

Batrachoseps attenuatus *Dispersal*.—We also explored the potential colonization of the Sutter Buttes by *B. attenuatus* from the Sierra Nevada foothills, given that it is the best supported hypothesis based on our available data. This scenario requires that the species cross the Great Central Valley twice. The first was presumably from the Diablo Range within the Coast Ranges to the Sierra Nevada foothills via the Trans-Valley Leak (Martínez-Solano et al., 2007), followed by a second dispersal from the Sierra Nevada foothills to the Sutter Buttes (Fig. 2, arrows).

The Trans-Valley Leak occurs for this species, and the other woodland herpetofauna, at a single discrete location, here represented by locality MS_59 (Figs. 2, 3; Jockusch, 1997; Martínez-Solano et al., 2007). The reason for this is unknown, but others have speculated that a climatic corridor existed in this area (Grinnell and Camp, 1917; Dunn, 1926; Peabody and Savage, 1958; Moritz et al., 1992), likely during the Pleistocene, as the species displaying this geographic leak pattern show limited genetic differentiation from presumed parental populations (Kuchta et al., 2009).

One possible explanation for the location of the Trans-Valley Leak may be an ancient, but no longer surface-observable, feature known as the Stockton Arch that was present at approximately the same location (Hackel, 1960; Repenning, 1960; Bartow, 1991). The Stockton Arch was an area of relative upland that separated the northern San Joaquin Basin from the southern Sacramento Basin (Hoots et al., 1954; Bartow, 1991). During the Pleistocene, Lake Clyde would have experienced episodic changes in depth through glacial and interglacial periods that occurred during the era of Great Central Valley inundation (Lisiecki and Raymo, 2005). During these fluctuations, it is likely the Arch was exposed for a few thousand years as Clyde Lake bifurcated into the Sacramento and San Joaquin Basins, which may have allowed for a connecting corridor of upland between the Coast Ranges and Sierra Nevada foothills (Sarna-Wojcicki, pers. comm.).

The second hypothesized dispersal of *B. attenuatus* from the Sierra Nevada foothills to the Sutter Buttes likely occurred along riparian corridors from the Feather River to the east. *Batrachoseps attenuatus* is found along the tributaries of the Sacramento and San Joaquin rivers today as population isolates in areas of relative upland above extant floodplains (Stebbins, 2003; Stebbins and McGinnis, 2012). The presence of these relic populations, some of which are well within the Great Central Valley, provides support for the interpretation that colonization of the Sutter Buttes took place by migrants from the foothills along riparian corridors.

The exact method and timing of how *B. attenuatus* was able to traverse the Great Central Valley remain a mystery without additional fossil and molecular data. A lack of available calibration points and the limits of single-gene molecular clock dating (McCormack et al., 2011) preclude our determination of whether *B. attenuatus* colonized the Sutter Buttes between their formation, beginning 1.59 mya and the formation of Lake Clyde, or whether connectivity with Sierra Nevada populations has been intermittently maintained throughout the Late Pleistocene and Holocene. There are few late Cenozoic fossil beds available to calibrate *B. attenuatus* movements in northern California, and small amphibians rarely fossilize (Hadley and Feranec, 2016). A *Batrachoseps* spp. vertebra has been found in Contra Costa County (Clark, 1985), and trackways and vertebrae have been documented east of the Great Central Valley (Peabody, 1959; Clark, 1985). However, identification of these fossils to the species level is not possible, and improper placement of these fossils in the phylogeny would seriously mislead dating inferences.

Sutter Buttes' Population Threats.—The Sutter Buttes *B. attenuatus* population is threatened by climate change, invasive species (Feral Pigs; *Sus scrofa*), and potential genetic isolation and inbreeding in the long term (Olson et al., 2016). Most sources consider *B. attenuatus* to be abundant wherever found (Cope, 1883; Hubbard, 1903; Burke, 1911; Stebbins and McGinnis, 2012). However, in the Sutter Buttes, the species is apparently rare (Anderson, 2004; Olson et al., 2016; Olson, pers. obs.). This may indicate low population sizes or perhaps a propensity toward greater fossorial activity in response to the Sutter Buttes relatively xeric climate. Based on a relatively intensive field sampling survey (Olson, 2007; Olson et al., 2016), our current working hypothesis is that the Sutter Buttes population is uncommon and potentially at risk. However, without a more detailed study of this population's demography, combined with a more comprehensive multi-gene phylogenetic analysis, we do not feel it is appropriate to make any specific conservation recommendations at this time. However, given their apparent rarity, isolation, and genetic distinctiveness, resource managers may follow the precautionary principle and take action to monitor and potentially manage this distinctive, isolated element of the California amphibian fauna.

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Supplementary Data

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