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FOUR NEW SPECIES OF CALIFORNIA LEGLESS LIZARDS (*ANNIELLA*)

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ABSTRACT. A previous genetic study of the California legless lizard (*Anniella pulchra*) revealed five deep genetic lineages and alluded to morphological differences among them. Here we show that three of these genetic lineages can be readily diagnosed from topotypic *A. pulchra* through a combination of coloration, scalation, and skeletal characters (trunk vertebra number). A fourth lineage is cryptic, but can be diagnosed from *A. pulchra* by its karyotype. We argue that these genetic clades of *A. pulchra* are strong candidates for species recognition because they exhibit properties that corroborate the DNA evidence for lineage separation. We therefore hypothesize that each of the five genetic clades of *A. pulchra* ("*Anniella* clades A–E") are distinct species and so describe four new species (*Anniella alexanderae*, sp. nov., *Anniella campi*, sp. nov., *Anniella grinnelli*, sp. nov., and *Anniella stebbinsi*, sp. nov.). In naming these new species we have chosen to honor four natural historians whose contributions to the study of California's vertebrate biodiversity are an ongoing inspiration for students of natural history and natural history museum curators. Two of these new species have small and poorly characterized ranges in the San Joaquin Valley and Carrizo Plain (*A. alexanderae* and *A. grinnelli*). A third restricted-range species (*A. campi*) is known from just three sites in the eastern Sierra Nevada. The fourth new species (*A. stebbinsi*) is a wide-ranging cryptic lineage that occurs throughout Southern California and into Baja California, Mexico. The limited distribution and fragile habitats occupied by the new species of *Anniella* warrant additional scientific research and conservation attention.

KEY WORDS: *Anniella pulchra*; California; conservation; lizard; new species

INTRODUCTION

The genus *Anniella* Gray, 1852, includes limbless lizards endemic to western North America. *Anniella* is the last survivor of an anguimorph lineage that first appeared in the Eocene of the western interior (Gauthier, 1982; Smith, 2011). From the Miocene on, the fossil record is restricted to within the known range of extant *Anniella* in California and Baja California, Mexico (Gauthier, 1980; Bell *et al.*, 1995; Hunt, 2008a). The populations traditionally assigned to the type species, *Anniella pulchra* Gray, 1852, occur

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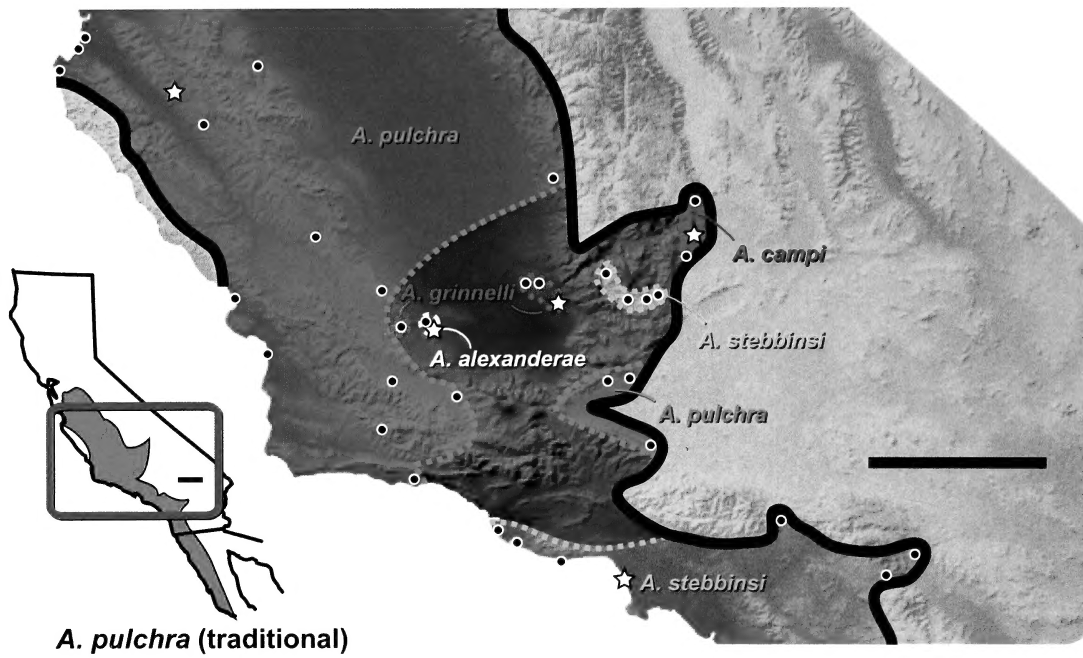

Figure 1. Map showing the traditional (inset) distribution of *Anniella pulchra* and a detail (main) showing the hypothesized distribution of the newly described species. White stars indicate type localities, black dots show referred specimens used in this study. Color-shaded areas are speculated based on the distribution of museum specimens and genetic clades (Parham and Papenfuss, 2009) updated through the addition of MVZ 172784 from the southern Sierra Nevada (*A. campi*, referred by morphology) and two genetically characterized specimens of *A. pulchra sensu stricto*: 1) SBMNH HE-2448 from within the Santa Barbara city limits; 2) MVZ 13376 (*A. pulchra sensu stricto*) based on data from Pearse and Pogson (2000). Contact zones between *A. pulchra* and the newly described species in the Carrizo Plain, San Joaquin Valley, Transverse Ranges, and Sierra Nevada are uncertain and so are not shaded. Scale bars = 100 km.

from northwest Baja California, to the eastern San Francisco Bay Area (Stebbins, 2003; Hunt, 2008c; Fig. 1). A second species, *Anniella geronimensis* Shaw, 1940, is restricted to coastal sand dunes in northwest Baja California, Mexico. There is a limited area of sympatry in Baja California in the vicinity of San Quintin Bay (Shaw, 1953; Hunt, 2008b).

Like other fossorial taxa with reduced or missing limbs, *Anniella* species are morphologically conservative. Hunt (1984) performed a study of morphological variation among *A. pulchra* populations. His detailed study, combined with our own observations, confirms that there are few significant differences in scalation among populations of *A. pulchra* (Table 1). The major morphological variation within *A. pulchra* is coloration, with some coastal populations showing dorsal melanism (Hunt, 1984, 2008a,c). Previous genetic studies of *A. pulchra* show that melanistic populations do not form a monophyletic group or correspond to the deepest genetics divergences (Bezy and Wright, 1971; Bezy *et al.*, 1977; Pearse and Pogson, 2000; Parham and Papenfuss, 2009).

We would expect that the reduced vagility associated with a subterranean ecology would facilitate speciation. Indeed, numerous genetic studies have shown that other morphologically conservative, fossorial, reptile taxa harbor cryptic species (e.g., Daniels

TABLE 1. SUMMARY OF NINE SCALE CHARACTERS FOR THE *ANNIELLA PULCHRA* COMPLEX.

	No. of Scales or Scale Rows[a]								
Anniella spp.	Supralabials	Infralabials	Dorsal	Ant.	Mid.	Post.	A. clear	M. clear	P. clear
Hunt (1984)[b]									
A. pulchra	5–7	5–8	198–250	31–36	28–32	22–26	4–8	4–7	3–5
A. stebbinsi	6–8	4–9	188–249	28–36	24–30	22–26	4–7	4–6	3–6
Holotypes[c]									
A. alexanderae	6	5	257	32	26	24	6	4	4
A. campi	5	5	244	35	32	27	5	4	4
A. grinnelli	6	5	239	30	25	23	7	5	6
A. stebbinsi	6	4	215	30	28	24	6	5	5

[a]Supralabials: number of supralabials; Infralabials: number of infralabials; Dorsal: number of dorsal scales counted along the midline; Ant.: number of anterior scale rows counted at two head lengths posterior to the interoccipital; Mid.: number of scale rows at mid-body; Post: number of posterior scale rows counted at 10 scales anterior to vent; A. clear: number of anterior clear scale rows (i.e., lacking dark pigmentation) between the dorsal and lateral stripes counted at two head lengths posterior to the interoccipital; M. clear: number of clear scale rows (i.e., lacking dark pigmentation) between the dorsal and lateral stripes at mid-body; P. clear: number of posterior clear scale rows (i.e., lacking dark pigmentation) between the dorsal and lateral stripes rows counted at 10 scales anterior to vent.

[b]Summary of data from Hunt (1984) based on 102 *A. pulchra* and 614 *A. stebbinsi*. Data included are from the clearly designated groups in that study that do not include more than one species. For *A. pulchra*, the groups included are: 1–3, 4, 7, 10. For *A. stebbinsi*, the groups included are: 12, 14–27. The following groups were excluded because they span geographic regions that may contain more than one species: 5, 6, 8, 9, 11, 13.

[c]Data from the holotypes of the new species described in this paper.

et al., 2009; Mott and Vietes, 2009; Heideman *et al.*, 2011). A similar pattern was not revealed in *Anniella* until our range-wide study of genetic variation among populations of *Anniella* (Parham and Papenfuss, 2009). In that paper, we reported mitochondrial and nuclear DNA sequences from 45 localities spanning the range of *A. pulchra*. Our data revealed five genetic clades that can be diagnosed with mitochondrial and nuclear DNA markers. The maximum uncorrected mitochondrial sequence divergence among the five genetic lineages of *A. pulchra* ranges from 4.3% to 9.2% (Parham and Papenfuss, 2009). This amount of divergence corresponds to species level differences of other lizard genera (reviewed by Papenfuss *et al.*, 2001). But more significantly, the genetic clades we uncovered can be diagnosed with morphological characters, including previously unreported coloration, vertebral counts from x-rays, or published karyotypic differences. Thus, unlike the aforementioned melanistic populations, the deep genetic clades of *A. pulchra* are strong candidates for species recognition because they exhibit properties that corroborate the genetic evidence for lineage separation (de Queiroz, 2007). We therefore hypothesize that each of the five genetic clades of *A. pulchra* (*Anniella* clades A–E of Parham and Papenfuss [2009]) are distinct species.

Before describing four new species, it is necessary to establish which of the five clades will remain as *A. pulchra*. Murphy and Smith (1991) designated a neotype for *A. pulchra* because of problems associated with the original description of the genus and species noticed by Hunt (1983). The neotype of *A. pulchra*, MVZ 64656, is from Pinnacles National Monument, San Benito County, California (Figs. 1, 2). A topotypic specimen, MVZ 247489, belongs to clade A, which is distributed throughout Northern California. Therefore, *A. pulchra* is now

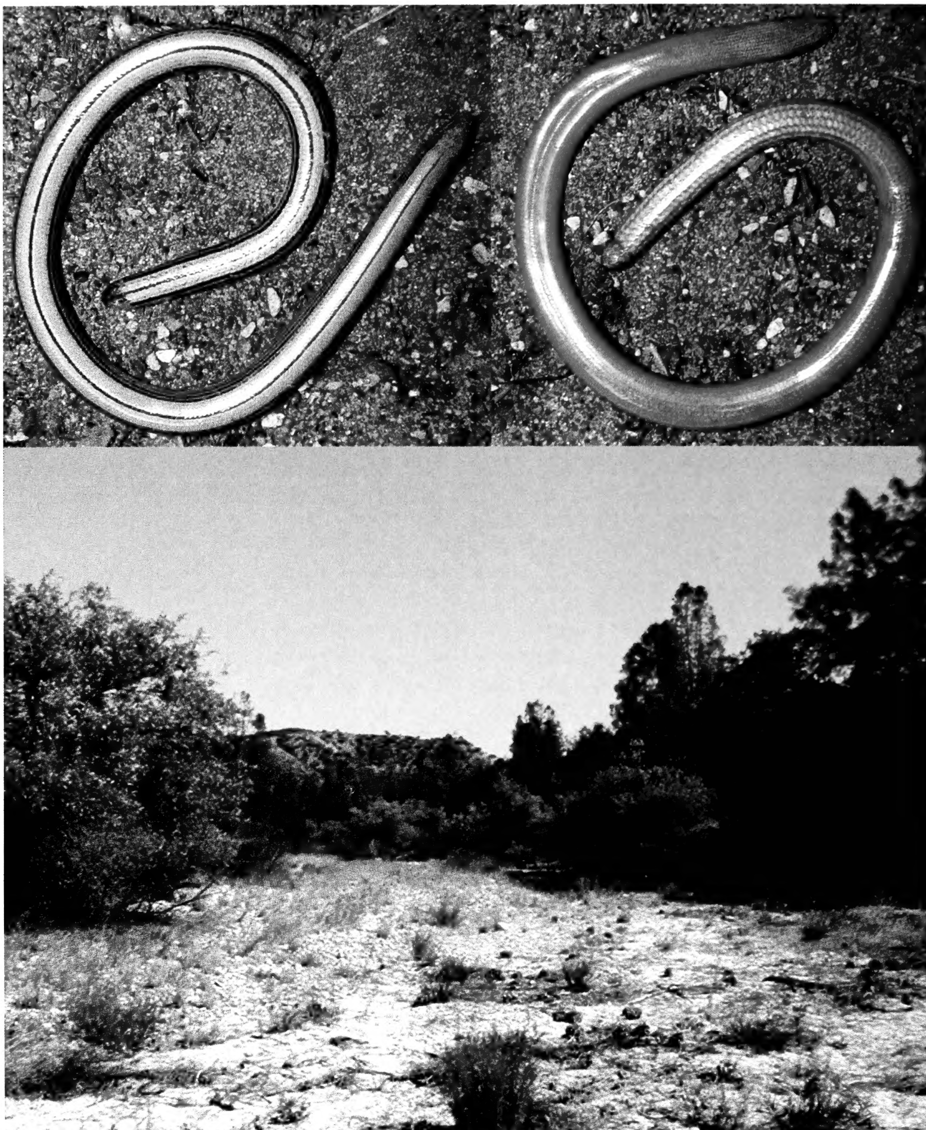

Figure 2. A topotypic *Anniella pulchra* (MVZ 247488) in dorsal and ventral views, and the type locality for the species at Pinnacles National Monument, San Benito County, California, U.S.A.

limited to populations in clade A of Parham and Papenfuss (2009). As such, genetic clades B–E are described as new species below. In naming these new species we have chosen to honor four natural historians whose contributions to the study of California's vertebrate biodiversity are an ongoing inspiration for students of natural history and natural history museum curators.

MATERIALS AND METHODS

Museum abbreviations: CAS, California Academy of Sciences, San Francisco, California; LACM, Natural History Museum of Los

TABLE 2. DIAGNOSTIC CHARACTERS FOR THE *ANNIELLA PULCHRA* COMPLEX. BOLD CHARACTER STATES DIAGNOSE THE NEW SPECIES FROM *A. PULCHRA*.

	A. pulchra	*A. alexanderae*	*A. campi*	*A. grinnelli*	*A. stebbinsi*
Ventral color	Yellow	**Grey**	Yellow	**Purple**	Yellow
Lateral stripe	~Single	Single	**Double**	Single	~Single
Mean vertebral count	<77 (76.0)	**>81 (82.2)**	<77 (76.5)	**>81 (81.2)**	<77 (75.4)
Dorsal scales	≤250 (198–250)	**>250 (252–278)**	<250 (219–244)	<250 (234–249)	<250 (188–249)
Mean dorsal scales	222.3	**261.2**	227.6	242.4	213.7
Chromosomes	2n = 20	?	?	?	**2n = 22**
Maximum ND2 divergence from *A. pulchra* (%)[a]	—	**8.0**	**8.4**	**9.2**	**8.7**

[a]Max. ND2 divergence from *A. pulchra* is the maximum sequence divergence from *A. pulchra* based on the mitochondrial DNA marker used by Parham and Papenfuss (2009). See descriptions and diagnoses of each species for more details.

Angeles, Los Angeles, California; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, California; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, California; SDNHM, San Diego Natural History Museum, San Diego, California; UCMP, University of California Museum of Paleontology, University of California, Berkeley, California. Locality data for all referenced material have been standardized into metric units and for format. Original locality information is available from the repositories.

Specimens used in the study were collected over a 14-year period. *Anniella* species are fossorial and are rarely active on the surface. Many of the sites sampled have no cover to search such as logs, stones, or leaf litter. More than 2,000 cover objects (flattened cardboard boxes and pieces of plywood) were placed at localities throughout the range of *Anniella* in California. Nearly all of the new species described here from sites north of the Transverse Ranges were found by raking in sandy soil under cover objects.

Molecular data used to delineate species here are taken from Parham and Papenfuss (2009). The samples from the Parham and Papenfuss (2009) study include all of the new holotypes and a topotype for *A. pulchra*. We refer closely related samples of each species by clade in the section called Referred Specimens (see below). We refer to the molecular marker sequenced by Parham and Papenfuss (2009), NADH dehydrogenase subunit 2 and five adjacent tRNAs (*trnWANCY*), as well as parts of cytochrome oxidase 1 and *trnM*, as "ND2" hereafter. Coloration data were taken from living specimens (Appendix) observed under a sunlight spectrum Bell & Howell lamp using a Munsell Book of Color (Munsell Color Company, 1976) and RGB Hexadecimal color conversions (Kelly and Judd, 1955) listed as "(Munsell, RGB)." Ventral coloration characters can only be observed in fresh specimens, whereas characters relating to the lateral stripes can be observed in preserved specimens. Vertebral counts were taken from x-rays (Appendix). Morphological abbreviations: SVL, snout-vent length; TL, tail length. Scale names in the descriptions are based on Smith (1946, p. 466). Scalation of the new holotypes was compared with a large survey of *A. pulchra* complex populations (Hunt, 1984; Table 1). Diagnostic characters are presented in Table 2.

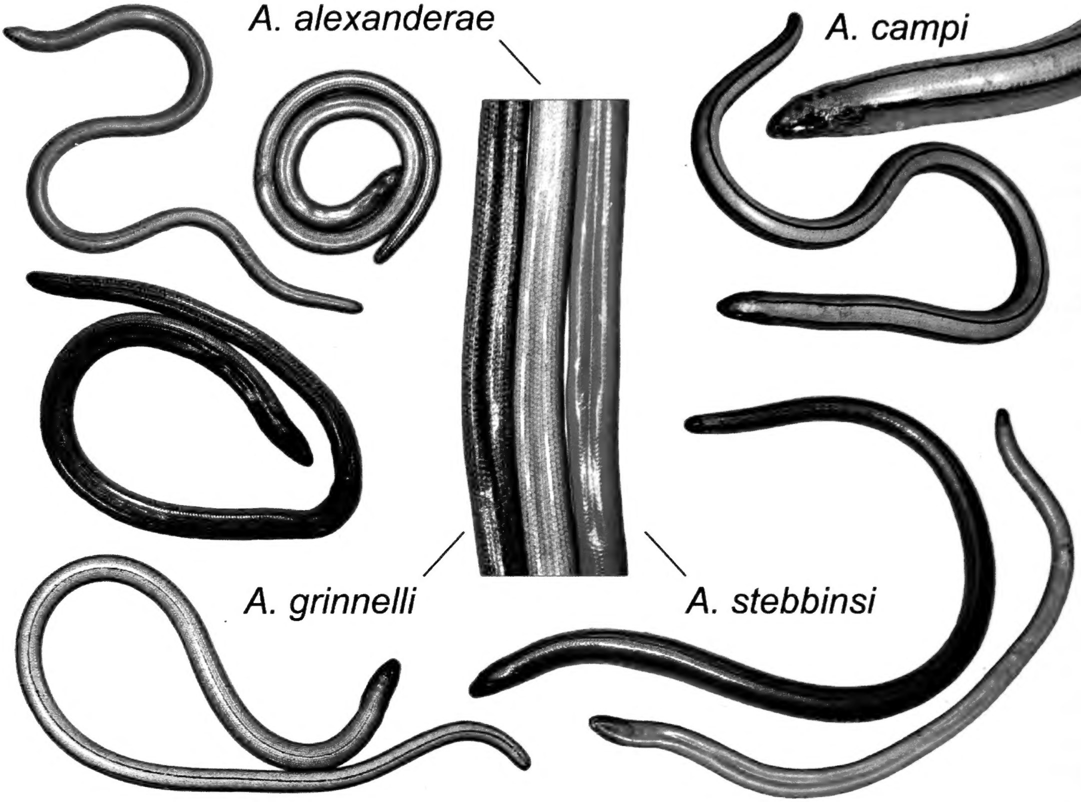

Figure 3. Four new species of *Anniella* and their diagnostic characters. Upper left, *Anniella alexanderae*: dorsal (MVZ 250549, paratype); ventral view showing the diagnostic gray coloration (MVZ 257720, paratype). Upper right, *Anniella campi*: dorsal (MCZ-R-189380, paratype); detail (MVZ 257277, holotype) showing diagnostic double dark lateral stripes. Lower left, *Anniella grinnelli*: ventral (MVZ 247487, paratype) showing diagnostic purple coloration; dorsal (MVZ 267228, paratype). Lower right, *Anniella stebbinsi*: dorsal (MVZ 250558, paratype); ventral (MVZ 267248). Center: comparison of ventral coloration from three of the new species. Left, *A. grinnelli* (MVZ 250546, paratype); center, *A. alexanderae* (MVZ 250549, paratype); right, *A. stebbinsi* (MVZ 250558, paratype).

Anniella alexanderae, new species
Temblor Legless Lizard
Figure 3

Anniella pulchra lineage B—Parham and Papenfuss, 2009.

Holotype. MVZ 250570, an adult male from 35.2090°N, 119.5672°W (380 m elevation [elev.]; Figs. 1, 4), Shale Rd., 1.3 km S (by road) junction with Hwy. 33, Kern County, California, U.S.A., collected on February 21, 2005, by Theodore J. Papenfuss and James F. Parham.

Paratypes. CAS 238588, an adult male from 35.2101°N, 119.5670°W (375 m elev.; Figs. 1, 4), Shale Rd., 1.3 km S by road of the junction with Hwy. 33, Kern County, California, U.S.A., collected on October 2, 2007, by Theodore J. Papenfuss; MCZ R-189386 and MVZ 267237, both adult males from 35.2092°N, 119.5671°W (413 m elev.; Figs. 1, 4), Shale Rd. 1.3. km S by road of the junction with Hwy. 33 (Figs. 1, 4), Kern County, California, U.S.A., collected on April 18, 2010, by Theodore J. Papenfuss;

Figure 4. Type localities of the four new species of *Anniella*. Upper left, *Anniella alexanderae*: Shale Rd., 1.3 km S (by road) junction with Hwy. 33, Kern County, California, U.S.A. Upper right, *Anniella campi*: Big Spring, 5.8 km NW junction Hwy. 14 (by Hwy. 178) Kern County, California, U.S.A. Lower left, *Anniella grinnelli*: Jack Zaninovich Memorial Nature Trail, Sand Ridge Preserve, Kern County, California, U.S.A. Lower right, *Anniella stebbinsi*: El Segundo Dunes, Los Angeles International Airport, Los Angeles County, California, U.S.A.

MVZ 250549 (Fig. 3), an adult male from 35.2090°N, 119.5666°W (380 m elev.; Figs. 1, 4), Shale Rd. 1.3. km S by road of the junction with Hwy. 33, Kern County, California, U.S.A., collected on October 21, 2005, by Theodore J. Papenfuss; MVZ 257720 (Fig. 3), an adult, not sexed, from 35.2090°N, 119.5666°W, (380 m elev.; Figs. 1, 4), Shale Rd., 1.3 km S by road of the junction with Hwy. 33, Kern County, California, U.S.A., collected April 2, 2007, by Theodore J. Papenfuss.

Referred Specimens. Additional specimens listed in the Appendix of this study and from clade B of Parham and Papenfuss (2009; localities 22 and 23 in the appendix of that study).

Diagnosis. Distinguished from all other species of the *A. pulchra* complex by a unique ventral coloration of Light Gray (5Y 7/1, RGB #D3D3D3) that is continuous from the insertion of the lower jaw to the end of the tail. This coloration is present in all paratypes and referred specimens. It is further distinguished from *A. pulchra*, *Anniella stebbinsi*, and *Anniella campi* by its higher vertebral count (Fig. 5) and from all species of the complex by its higher dorsal scale count (Tables 1, 2). *Anniella alexanderae* shows a maximum mitochondrial

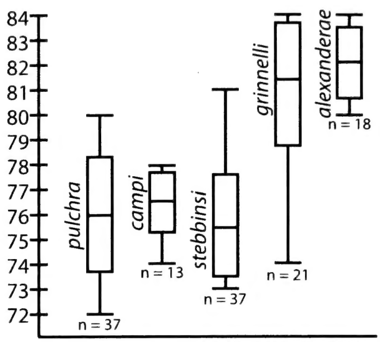

Figure 5. Box and whisker plots (range, sample standard deviation, mean) of trunk vertebral counts of *Anniella pulchra* and the four new species based on x-ray images of museum specimens. *Anniella alexanderae* and *Anniella grinnelli* show higher vertebral counts than the other three species of the *A. pulchra* complex. Note that a single outlier with a trunk vertebral count of 74 (the rest are 79–84) affects the range of *A. grinnelli*.

sequence divergence (for ND2, see Materials and Methods) from *A. pulchra* of 8.0%, from *A. grinnelli* of 6.0%, from *A. campi* of 4.9%, and from *A. stebbinsi* of 4.9% (Parham and Papenfuss, 2009).

Description (Based on Holotype). Adult male, 158 mm SVL, 81 mm TL; 81 trunk vertebrae. Coloration in life: dorsal color Pale Olive (5Y 6/4, RGB #A79367), lateral color Strong Orange (5YR 7/12, RGB #A85400), ventral color ventral Light Gray (5Y 7/1, RGB #D3D3D3); a mid-dorsal black stripe one-third scale wide is present from the parietals to the tip of the tail; lateral black stripes one-third scale wide are present from the eye to the tip of the tail.

Rostral large, visible from above; posterior tip pointed and in contact with prefrontals in a slight groove at anterior suture of prefrontals; supraoculars 3-3; preoculars 1-1; postoculars 2-2; occipitals 2-2; supralabials 6-6, first small and located directly beneath nasal with posterior edge in contact with second supralabial, second largest, third and fourth half the length of second and in contact with eye, fifth equal in size to third and fourth and in contact with postoculars; anterior two-thirds of mental contacts first pair of infralabials, posterior pointed one-third of mental inserts in a groove between postmentals; infralabials 5-5; 32 scale rows two head lengths posterior to the interoccipital, 26 scale rows at mid-body; 24 scale rows counted 10 scales anterior to vent; six clear (no dark pigment from stripes) scale rows between dorsal and lateral stripe on right side of body two head lengths posterior to the interoccipital; four clear scale rows at mid-body, four clear scale rows at a point 10 scales anterior to vent; 257 dorsal body scales counted along right side of mid-dorsal line from posterior border of interoccipital to a point above the vent.

Distribution. This species is known from two sites separated by continuous suitable habitat west of Hwy. 33. The known sites are in areas of sandy soil at the southeast base of the Temblor Range between McKittrick and Taft on the west side of the Southern San Joaquin Valley in Kern County, California (Fig. 1). All specimens have been found between California State Highway 33 and the Temblor Range. Detailed searches, including multi-year use of cover boards, have failed to yield *Anniella* in apparent suitable habitat on the floor of the San Joaquin Valley east of Highway 33.

Natural History. All specimens were found under cover boards and flattened cardboard boxes placed on sandy soil. This species is most easily found between February and March when the soil is damp. The known range is in an arid part of California (average annual rainfall at nearby McKittrick is just 184 mm).

Etymology. This species is named after the naturalist Annie Montague Alexander (1867–1950; Fig. 6), who collected thousands of botanical, paleontological, and zoological specimens from western North America and provided intellectual support and crucial endowments for both the Museum of Vertebrate Zoology and the Museum of Paleontology at

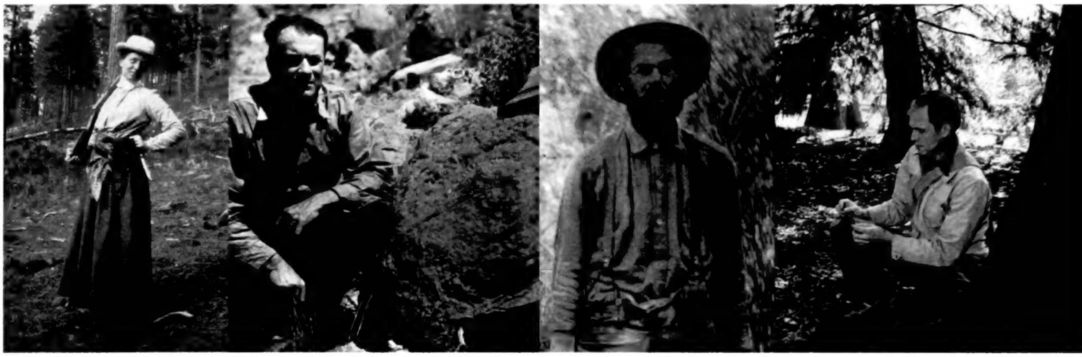

Figure 6. Four natural historians whose contributions to the study of California's vertebrate biodiversity are honored by the new species of *Anniella* described here. Left, Annie Montague Alexander (1867–1950) on expedition collecting Pleistocene fossils at Fossil Lake, Lake County, Oregon, in 1901 (from the UCMP archives). Center left, Charles Lewis Camp (1893–1974) on expedition in San Juan County, Utah, in 1942 (from the UCMP archives) next to the holotype of the Permian tetrapod *Tseajaia campi* Vaughn, 1964. Center right, Joseph Grinnell (1877–1939) on expedition collecting vertebrates in Imperial County, California, in 1910 (from the MVZ archives). Robert Cyril Stebbins (1915–) with an *Ensatina* salamander on the University of California at Berkeley campus in 1951 (from the MVZ archives).

the University of California at Berkeley (Stein, 2001).

***Anniella campi*, new species**
Southern Sierra Legless Lizard
Figure 3

Anniella pulchra lineage D—Parham and Papenfuss, 2009.

Holotype. MVZ 257727 (Fig. 3) from 35.6251°N, 117.9581°W (1,230 m elev.; Figs. 1, 4), Big Spring, 5.8 km NW Junction Hwy. 14 (by Hwy. 178) Kern County, California, U.S.A., collected on March 31, 2006, by Theodore J. Papenfuss.

Paratypes. CAS 233827, an adult male, 233828, an adult female, from 35.6252°N, 117.9581°W (1,240 m elev.; Figs. 1, 4), Big Spring, 5.8 km NW junction Hwy. 14 (by Hwy. 178) Kern County, California, U.S.A., collected on March 31, 2006, by Theodore J. Papenfuss; MCZ R-189380 (Fig. 3), 189381, 189382, adults not sexed from 35.6252°N, 117.9581°W (1,240 m elev.; Figs. 1, 4), Big Spring, 5.8 km NW junction Hwy. 14 (by Hwy. 178) Kern County, California, U.S.A., collected on May 7, 2011, by Theodore J. Papenfuss.

Referred Specimens. MVZ 172784 (Kern County, California, U.S.A.), additional specimens listed in the Appendix of this study and from clade D of Parham and Papenfuss (2009; localities 28 and 29 in the appendix of that study).

Diagnosis. Distinguished from all other species of the *Anniella pulchra* complex by a unique color pattern consisting of continuous, double, dark lateral stripes from the side of the head to the tip of the tail. This character is present in all paratypes and referred specimens. *Anniella campi* shows a maximum mitochondrial sequence divergence (for ND2, see Materials and Methods) from *A. pulchra* of 8.4%, from *A. grinnelli* of 5.8%, from *A. alexanderae* of 4.9%, and from *A. stebbinsi* of 4.3%.

Description (Based on Holotype). Adult male, SVL 152 mm, regenerated TL 60 mm, 74 trunk vertebrae. Coloration in life: dorsal color Yellowish Gray (2.5Y 7/2, RGB #C1AE96), lateral color Vivid Yellow (5Y 7/12, #DBA600), ventral color Vivid Yellow (5Y 8/14, RGB #FBCE00).

Rostral large, visible from above. Posterior tip pointed and in contact with prefrontals in a slight groove at anterior suture of prefrontals; supraoculars 3-3; preoculars 1-1; postoculars 2-2; occipitals 2-2; supralabials 5-5, first small and located directly beneath nasal with posterior edge in contact with second supralabial, second largest, third, fourth, and fifth half the length of second, third and fourth in contact with eye; anterior two-thirds of mental contacts first pair of infralabials, posterior pointed one-third of mental inserts in a groove between postmentals; infralabials 5-5; 35 scale rows two head lengths posterior to the interoccipital, 32 scale rows at mid-body; 27 scale rows counted 10 scales anterior to vent; five clear scale rows between dorsal and lateral stripe on right side of body two head lengths posterior to the interoccipital; four clear (no dark pigment from stripes) scale rows at mid-body, four clear scale rows at a point 10 scales anterior to vent; 244 dorsal body scales counted along right side of mid-dorsal line from posterior border of interoccipital to a point above the vent.

Distribution. Anniella campi is only known from thee localities along the western edge of the Mojave Desert in Kern and Inyo counties (Fig. 1). The Big Spring locality is a permanent spring that supports a small area of suitable habitat, estimated at less than 2 hectares, in an otherwise desert environment. The *Anniella* population here is clearly relictual since there is no other suitable habitat in the area. Parham and Papenfuss (2009) reported a second along Nine Mile Canyon Road in southern Inyo County, north of Big Spring. A third locality, south of Big Spring in Kern County is represented by a museum specimen that shows the diagnostic character of the complete double lateral stripes (MVZ 172784). Specimens have been found crossing the road at night (Robert W. Hansen, personal communication). It is likely that this species will be found in canyons between Big Spring and Nine Mile Canyon.

Natural History. This species is locally common at Big Spring, where specimens have been collected by raking under debris that has accumulated at the base of Chamisa (*Ericameria nauseosa*) that grow adjacent to the spring. Specimens have been found in April and May.

Etymology. This species is named after Charles Lewis Camp (1893–1974; Fig. 6), former student at the Museum of Vertebrate Zoology and later director of the University of California Museum of Paleontology. On a 1915 collecting expedition to Yosemite National Park with Joseph Grinnell, he discovered the Mt. Lyell salamander, *Hydromantes platycephalus* (Camp, 1916), part of a lineage that is otherwise restricted to the Old World and therefore one of the more significant herpetological discoveries in North America. Charles Camp also participated in successful paleontological expeditions throughout western North America, as well as Africa, Australia, and South America. Camp's (1923) influential "Classification of the lizards" formed the foundation for modern taxonomy of squamates (Estes and Pregill, 1988).

***Anniella grinnelli*, new species**
Bakersfield Legless Lizard
Figure 3

Anniella pulchra lineage C—Parham and Papenfuss, 2009.

Holotype. MVZ 257714, from 35.3054°N, 118.8013°W (254 m elev.; Figs. 1, 4), Jack Zaninovich Memorial Nature Trail, Sand Ridge Preserve, Kern County, California, U.S.A., collected on April 11, 2007, by James F. Parham and Theodore J. Papenfuss.

Paratypes. CAS 234253, an adult male, CAS 234254 and 234255, both adult females, from 35.3894°N, 119.0697°W (130 m elev.), in a field 0.8 km N of Rosedale Hwy. by Fruitvale Ave then 0.3 km E of the end of Price Way, Bakersfield, Kern County, California, collected on February 1, 2006, by James F. Parham and Theodore J. Papenfuss; MCZ R-189378, R-189379, adult males from 35.3900°N, 119.0608°W (125 m elev.), 0.65 km N of Rosedale Hwy. by Landco Dr., then 0.15 km W at end of Gilmore Ave., Bakersfield, Kern County, California, collected on April 21, 2010, by Theodore J. Papenfuss; MVZ 247487 (Fig. 3), an adult, not sexed, from 35.3894°N, 119.0697°W (120 m elev.) in a field 0.8 km N of Rosedale Hwy. by Fruitvale Ave then 0.3 km E of the end of Price Way, Bakersfield, Kern County, California, U.S.A., collected on April 27, 2002, by Theodore J. Papenfuss; MVZ 250546 (Fig. 3), an adult female from 35.3900°N, 119.0608°W (125 m elev.), 0.65 km N of Rosedale Hwy. by Landco Dr., then 0.15 km W at end of Gilmore Ave., Bakersfield, Kern County, California, collected on April 21, 2010, by Theodore J. Papenfuss; MVZ 267228 (Fig. 3), an adult, not sexed, from 35.3894°N, 119.0697°W (120 m elev.) in a field 0.8 km N of Rosedale Hwy. by Fruitvale Ave. then 0.3 km E of the end of Price Way, Bakersfield, Kern County, California, U.S.A., collected on March 17, 2005, by Theodore J. Papenfuss.

Referred Specimens. Additional specimens listed in the Appendix of this study and from clade C of Parham and Papenfuss (2009; localities 24 through 27 in the appendix of that study).

Diagnosis. Distinguished from all other species of *Anniella* by a unique ventral coloration of Grayish Red (2.5R 4/2, RGB #755A61). This coloration is continuous from the anterior end of the lower jaw to the end of the tail and is present in all paratypes and known specimens. It is further distinguished from *A. pulchra*, *A. stebbinsi*, and *A. campi* by its higher vertebral count (Fig. 5). *Anniella grinnelli* shows a maximum mitochondrial sequence divergence (for ND2, see Materials and Methods) from *A. pulchra* of 9.2%, from *A. stebbinsi* of 6.4%, from *A. alexanderae* of 6.0%, and from *A. campi* of 5.8%.

Description (Based on Holotype): Adult male, 148 mm SVL, 93 mm TL; 79 trunk vertebrae. Coloration in life: dorsal color Light Olive Gray (7.5Y 5/2, RGB #837A67), lateral color Strong Orange (5YR 7/12, RGB #A85400), ventral color Grayish Red (2.5R 4/2, RGB #755A61 [appears purple]); a mid-dorsal black stripe one-half scale wide is present from the parietals to the tip of the tail; lateral black stripes one scale wide are present from the eye to the tip of the tail.

Rostral large, visible from above, posterior side flat and in contact with prefrontals; supraoculars 3-3; preoculars 1-1; postoculars 2-2; occipitals 2-2; supralabials 6-6, first small and located directly beneath nasal, second largest, third and fourth half the length of second and in contact with eye; mental rounded and broadly in contact with first pair of infralabials and postmentals; infralabials 5-5; 30 scale rows two head lengths posterior to the interoccipital, 25 scale rows at mid-body; 23 scale rows counted 10 scales anterior to vent; seven clear (no dark pigment from stripes) scale rows between dorsal and lateral stripe on right side of body two head lengths posterior to the interoccipital; five clear scale rows at mid-body, six clear scale rows at a point 10 scales anterior to vent; 239 dorsal body scales counted along right side of mid-dorsal line from posterior border of interoccipital to a point above the vent.

Distribution. This known range of *A. grinnelli* is restricted to the southern San Joaquin Valley and the east side of the Carrizo Plain (Fig. 1). Specimens have been collected within the city limits of Bakersfield. During the last 10 years, two of the three known Bakersfield populations were destroyed by housing development. A protected population is located at the type locality, the

Sand Ridge Preserve. Individuals from the Carrizo Plain are similar in coloration and mitochondrial sequences to San Joaquin samples but have a nuclear genotype known only from lineage B. Parham and Papenfuss (2009) speculated that this population may be a hybrid or intergrade population, but we include Carrizo specimens in our concept of *A. grinnelli* (Fig. 1).

Natural History. All specimens were found under cover objects (plywood scraps and flattened cardboard boxes) that had been placed on sandy soil. The type locality is a stable sand dune of Pleistocene origin (Fig. 4).

Etymology. This species is named after Joseph Grinnell (1877–1939; Fig. 6), the first director of the Museum of Vertebrate Zoology at the University of California at Berkeley. Joseph Grinnell published hundreds of scientific papers based on his extensive collecting and surveys in western North America, and developed the Grinnell Method of note taking that has become the standard for natural history observations.

Anniella stebbinsi, new species
Southern California Legless Lizard
Figure 3

Anniella pulchra lineage E—Parham and Papenfuss, 2009

Holotype. MVZ 267246, from 33.9500°N, 118.4415°W (24 m elev.; Figs. 1, 4), El Segundo Dunes, Los Angeles International Airport, Los Angeles County, California, U.S.A., collected on April 20, 2010, by Theodore J. Papenfuss.

Paratypes. MVZ 267247, a subadult male collected with the holotype; MVZ 250558 (Fig. 3), a subadult male from 34.0042°N, 118.8100°W (5 m elev.), Point Dume, Los Angeles County, California, U.S.A., collected on November 24, 2005, by Theodore J. Papenfuss. MVZ 267248 (Fig. 3), from 33.9015°N, 116.7447°W (470 m elev.), 4.0 km SE (airline) of Cabazon, Riverside County, California, U.S.A., collected on March 19, 2005, by Theodore J. Papenfuss.

Referred Specimens: LACM 64583 (karyotyped specimen [Bezy *et al.*, 1977] from the type locality in Los Angeles County, California, U.S.A.), SDNHM 42040, 42041, 42876, 42878, 42879 (San Diego County, California, U.S.A.), additional specimens listed in the Appendix of this study, and from clade E of Parham and Papenfuss (2009; localities 30–45 in the appendix of that study, but excluding the *A. geronimensis* from locality 41 [Colonia Guerrero]).

Diagnosis. Distinguished by its yellow ventral coloration from *A. grinnelli*, which has a purple (grayish-red) ventral coloration and from *A. alexanderae*, which has a light gray ventral coloration. Distinguished from *A. pulchra* which also has a yellow ventral coloration by a somatic chromosome number of 2n = 20 rather than 2n = 22 (Bezy *et al.*, 1977). Distinguished from *A. campi*, which also has a yellow ventral coloration by a single dark lateral stripe on each side rather than a double lateral stripe. Some specimens of *A. stebbinsi* have a double lateral stripe, but it is never continuous or exceeds 50% of the combined body and tail length, whereas in *A. campi* it is continuous and extends to the tip of the tail. *Anniella stebbinsi* shows a maximum mitochondrial sequence divergence (for ND2, see Materials and Methods) from *A. pulchra* of 8.7%, from *A. grinnelli* of 6.4%, from *A. alexanderae* of 4.9%, and from *A. campi* of 4.3%.

Description (Based on Holotype). Adult female, SVL 132 mm, regenerated TL 81 mm, 79 trunk vertebrae. Coloration in life: dorsal color Light Olive Brown (2.5Y 5/2, RGB #8B7863), lateral color Strong Yellow (RGB #E1A129), ventral color Moderate Yellow (5Y 7/8, RGB #CFA639); mid-dorsal black stripe less than one scale wide is present from the parietals to the tip of the tail; lateral black stripes one scale wide are present from the eye to the tip of the tail.

Rostral large, visible from above, posterior tip pointed and in contact with prefrontals in a slight groove at anterior suture of prefrontals; supraoculars 3-3; preoculars 1-1; postoculars 2-2; occipitals 2-2; supralabials 6-6, first small and located directly beneath nasal with posterior edge in contact with second supralabial, second largest, third and fourth two-thirds the length of second and in contact with eye; mental rounded, broadly in contact with first pair of infralabials and postmentals; infralabials 4-4; 30 scale rows two head lengths posterior to the interoccipital, 28 scale rows at mid-body; 24 scale rows counted 10 scales anterior to vent; six clear (no dark pigment from stripes) scale rows between dorsal and lateral stripe on right side of body two head lengths posterior to the interoccipital; five clear scale rows at mid-body, five clear scale rows at a point 10 scales anterior to vent; 215 dorsal body scales counted on right side of mid-dorsal line from posterior border of interoccipital to a point above the vent; 215 dorsal body scales counted along right side of mid-dorsal line from posterior border of interoccipital to a point above the vent.

Distribution. Throughout Southern California south of the Transverse Ranges into northern Baja California, Mexico (Fig. 1). Populations in the Tehachapi and Piute mountains of Kern County are disjunct from the main distribution of this species to the south. Therefore, the distribution of *A. stebbinsi* is presumably bisected by southern populations of *A. pulchra* ranging from the Santa Barbara region into the Antelope Valley of the western Mojave Desert (Fig. 1; Parham and Papenfuss, 2009). Based on the bulk of their hypothesized range, we recommend the common names of "Northern California legless lizard" for *A. pulchra* and "Southern California legless lizard" for *A. stebbinsi*.

Natural History. Anniella stebbinsi is found in a broader range of habitats that any of the other species in the genus. Often locally abundant, specimens are found in coastal sand dunes and a variety of interior habitats, including sandy washes and alluvial fans (Stebbins and McGinnis, 2012). Much of the coastal dune habitat has been destroyed by coastal development between Ventura County and the Mexican Border. Fortunately, a large protected population persists in the remnant of the once extensive El Segundo Dunes at Los Angeles International Airport (Fig. 4).

Anniella stebbinsi is common at the western margin of the Colorado Desert under trash dumped at the base of Mt. San Jacinto in the vicinity of Cabazon, Riverside County. Here the only large shrub is Creosote (*Larrea tridentata*). The seasonal Whitewater River provides sufficient moisture near the surface. The disjunct northern populations occur in sandy soils in the Piute and Tehachapi mountains at elevations of 400–900 m in both Oak Woodland and Mixed Conifer Forest. In the lower drainage of Caliente Creek at Caliente Post Office, individuals have been collected beneath cardboard cover placed under Scalebroom bushes (*Lepidospartum squamatum*). There is continuous sandy habitat along Caliente Creek between Caliente Post Office and Sand Ridge Preserve, the type locality for *A. grinnelli.* Additional fieldwork is needed to document the location of an almost certain contact between these two species. Contact between *A. stebbinsi* and *A. pulchra* is likely along the coast of California between the cities of Santa Barbara and Oxnard and along the southeastern slope of the Tehachapi Mountains, where *A. pulchra* is common in Joshua/Juniper woodland.

Etymology. This species is named after Robert Cyril Stebbins (1915–; Fig. 6) who was appointed the first Curator of Herpetology at the Museum of Vertebrate Zoology in 1945. Robert Stebbins' contribution to western North American herpetology includes many scientific publications, but especially his classic, comprehensive, beautifully self-illustrated, and influential field guides (Stebbins 1951, 1954, 1960, 1966, 1972, 1985, 2003; Stebbins and McGinnis, 2012).

CONSERVATION IMPLICATIONS

The former *A. pulchra*, a species of special concern (Jennings and Hayes, 1994), is now divided into five species. This means *A. pulchra* has a smaller distribution than previously recognized, thereby enhancing concern about its conservation status. The remaining four species have even smaller ranges, some of which are degraded or threatened by human activities. Whereas much of the range of *A. stebbinsi* is already compromised by urban development, the conservation implications for the other three new species are even more striking because of their very limited distributions. *Anniella grinnelli* is known from a few sites in the southern San Joaquin Valley, an area that has been greatly modified by urban and agricultural development (PPIC, 2006; Great Valley Center, 2007). *Anniella grinnelli* persists in small patches within the Bakersfield city limits, but some of the populations we collected were extirpated by development during the course of this study. The type locality at the Sand Ridge Preserve is a secure site that will help ensure the species survival. *Anniella alexanderae* is known from two sites at the base of the Temblor Mountains, and should be considered rare pending further study. Finally, *Anniella campi* is known from just three sites. This species may be restricted to the vicinity of potentially fragile springs in canyons that open into the Mojave Desert and so warrants careful monitoring. Additional research into the distribution, contact zones, and diversity of *Anniella* is clearly needed.

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Appendix 1

The following specimens were used for the vertebral counts (shown in parentheses) summarized in Table 1 and 2: ***A. alexanderae***: CAS 238588 (82); MCZ R-189383 (84); MCZ R-189384 (83); MCZ R-189385 (82); MCZ R-189386 (82); MVZ 250528 (81); MVZ 250549 (83); MVZ 250550 (80); MVZ 250570 (81); MVZ 250573 (81); MVZ 250574(82); MVZ 250575 (83); MVZ 250576 (82); MVZ 257082 (84); MVZ 257717(84); MVZ 257718 (81); MVZ 257720 (82); MVZ 257741 (82). ***A. campi***: MCZ R-189380 (78); MCZ R-189381 (76); MCZ R-189382 (78); MVZ 104771 (76); MVZ 228817 (77); MVZ 228818 (77); MVZ 228819 (77); MVZ 228829 (78); MVZ 232844 (76); MVZ 257727 (74); MVZ 257728 (75); MVZ 257729 (78); MVZ 257730 (75). ***A. grinnelli***: MCZ R-189378 (79); MCZ R-189379 (83); MVZ 230663 (83); MVZ 230665 (74); MVZ 247487 (82); MVZ 250527 (84); MVZ 250534 (81); MVZ 250541 (81); MVZ 250542 (79); MVZ 250543 (86); MVZ 250545 (84); MVZ 250546 (83); MVZ 250547 (83); MVZ 250548 (82); MVZ 257714 (79); MVZ 257716 (80); MVZ 257724 (80); MVZ 257725 (80); MVZ 257726 (80); MVZ 257737 (82); MVZ 257738 (81). ***A. pulchra***: MVZ 27300 (73); MVZ 33793 (78); MVZ 33795 (76); MVZ 33796 (75); MVZ 33860 (73); MVZ 45612 (74); MVZ 58106 (75); MVZ 58410 (78); MVZ 60216 (74); MVZ 60292 (75); MVZ 64105 (76); MVZ 64106 (76); MVZ 71919 (75); MVZ 71920 (75); MVZ 71921 (74); MVZ 71922 (75); MVZ 84593 (73); MVZ 83594 (75); MVZ 117600 (75); MVZ 223384 (74); MVZ 227778 (73); MVZ 228815 (74); MVZ 228816 (75); MVZ 228832 (78); MVZ 247488 (72); MVZ 247489 (74); MVZ 250536 (78); MVZ 250537 (80); MVZ 250538 (79); MVZ 250539 (79); MVZ 250540 (78); MVZ 250562 (79); MVZ 250563 (78); MVZ 250564 (78); MVZ 250566 (79); MVZ 250567 (79); MVZ 250569 (79). ***A. stebbinsi***: MVZ 226854 (75); MVZ 226855 (75); MVZ 226856 (74); MVZ 226857 (77); MVZ 226859 (75); MVZ 226860 (76); MVZ 226863 (75); MVZ 228844 (75); MVZ 228861 (74); MVZ 230554 (77); MVZ 230556 (75); MVZ 230666 (76); MVZ 230667 (75); MVZ 230668 (77); MVZ 230669 (78); MVZ 230673 (81); MVZ 230674 (74); MVZ 230675 (73); MVZ 230676 (74); MVZ 230677 (74); MVZ 230678 (74); MVZ 232618 (77); MVZ 232619 (77); MVZ 232621 (76); MVZ 250552 (75); MVZ 250553 (73); MVZ 250577 (75); MVZ 250731 (74); MVZ 250732 (77); MVZ 250733 (76); MVZ 257743 (74); MVZ 257744 (73); MVZ 257745 (76); MVZ 274645 (78); MVZ 267246 (71); MVZ 267247 (71). The following specimens were used for the dorsal scale counts (shown in parentheses) summarized in Table 1 and 2: ***A. alexanderae***: MVZ 250528 (257); MVZ 250550 (255); MVZ 250570 (257); MVZ 250574 (263); MVZ 250576 (252); MVZ 257718 (268); MVZ 257720 (265); MVZ 257739 (256); MVZ 257741 (261); MVZ 267236 (278). ***A. campi***: MVZ 104771 (223); MVZ 172784 (227);

MVZ 228817 (230); MVZ 228818 (224); MVZ 228819 (222); MVZ 228820 (235); MVZ 228821 (223); MVZ 257727 (244); MVZ 257728 (219); MVZ 267231 (229). ***A. grinnelli*:** MVZ 230663 (234); MVZ 250527 (246); MVZ 250527 (246); MVZ 250534 (248); MVZ 250543 (234); MVZ 250546 (243); MVZ 250547 (249); MVZ 257714 (239); MVZ 257726 (247); MVZ 257742 (238). The following specimens were used to evaluate ventral coloration (see Materials and Methods): ***A. alexanderae*:** CAS 238588; MVZ 250570; MVZ 250549; MVZ 257739. ***A. campi*:** MVZ 257727; MVZ 257728. ***A. grinnelli*:** CAS 234252; MVZ 250546; MVZ 257718; MVZ 257737; MVZ 257738. ***A. pulchra*:** MVZ 257098; MVZ 257731; MVZ 257732. ***A. stebbinsi*:** MVZ 250552; MVZ 250553; MVZ 250556; MVZ 257723; MVZ 257735.

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