Catalogue of American Amphibians and Reptiles.

Hunt, L.E. 2006. Anniella pulchra.

Anniella pulchra Gray California Legless Lizard

Anniella pulchra Gray 1852:440. Type-locality, "0.8 km S of east entrance (California Highway 146) to Pinnacles National Monument, San Benito County, California". Neotype, University of California Museum of Vertebrate Zoology (MVZ) 64656, an adult male, collected by R.C. Stebbins on 17 March 1956 (examined by author). See Nomenclatural History.

Anniella pulchra: Richardson 1852:154 (not of Gray 1852). Specimen presumably lost (Hunt 1983).

Anniella nigra Fischer 1885:9. Type-locality, "close to San Diego, California", restricted by Schmidt (1953) to, "the vicinity of Pacific Grove, Monterey County, California." Holotype, British Museum (Natural History) (BMNH) 86.5.15.41, an adult male collected by J. Behrens, date unknown.

Anniella texana Boulenger 1887:50. Type-locality, "El Paso, Texas", restricted by Smith and Taylor (1950a,b) to "San Diego, California", and by Hunt (1983) to "the Monterey Peninsula, Monterey County, California." Holotype, British Museum (Natural History) (BMNH) 1946.8.29.27 (original number BMNH 87.5.12.36), an adult male, collected by A. Forrer, date unknown (examined by author).

Anniela pulchra: Baker 1987:236. Lapsus.

- **CONTENT**. Two subspecies, *pulchra* and *nigra*, are recognized.
- **DEFINITION**. Anniella pulchra is a small, elongate, fossorial, limbless lizard (adult SVL 95–170 mm, tail length 43–103 mm, tail 26%–42% of total length). Sexual dimorphism and dichromatism are absent. The snout is rounded in profile, there are 24–34 body scale rows at mid-body, 5–8 (typically 7) supralabials with the second supralabial scale being the largest, 4–8 scale rows between the vertebral and first lateral stripe, and 84–130 scales along the vertebral midline on the tail.

Color, pattern, body size, and scalation vary geographically (Hunt 1984). Populations inhabiting coastal dunes fringing southern Monterey Bay and on the Monterey Peninsula in Monterey County display a dark brown to jet-black dorsum and a relatively short tail (as a percentage of total length). Coastal populations from southwestern San Luis Obispo and western Santa Barbara County also display a dark brown dorsum, but are not jet-black and have relatively longer tails. Dorsal coloration in other coastal and interior populations ranges from metallic silver, silvery-green, copper, tan, to beige. Ventral coloration varies from whitish-yellow to bright chrome yellow. One or more brown or black stripes separate the dorsum and ventrum along the side of the body. These stripes coalesce along the sides of the head to form an eve





FIGURE 1. Anniella pulchra from Morro Bay, San Luis Obispo County, California (top) and Monterey County, California (bottom). Photos courtesy of Gary Nafis and CaliforniaHerps.com.

stripe in some populations. The preanal scales are tipped with brown or black and contrast with the surrounding solid yellow or whitish-yellow ventral body scales. A brown or brownish-black border occurs along the edges of the ventral tail scales, forming faint zigzag longitudinal stripes between the scale rows on the tail. A brown or black vertebral stripe is visible in most non-melanistic populations, although this may be faint or distinct.

- **DESCRIPTIONS**. Detailed descriptions of the external morphology of this species are found in Bocourt (1881), Boulenger (1887), Cope (1900), Fischer (1885), Fisher (1934), Grismer (2002), Hunt (1983, 1984), Miller (1944), Richardson (1852), Rieppel (1978), Shaw (1940, 1950), Smith (1946), Stebbins (1954, 2003), and Van Denburgh (1897, 1905, 1922). Grinnell and Camp (1917), Klauber (1940), and Miller (1943) described intergrades between the subspecies. Bezy et al. (1977) describe karyotypic variation.
- ILLUSTRATIONS. Line drawings and/or color illustrations of scalation, coloration, pattern, external and internal morphology are found in Anonymous (1982), Bettelheim (2005), Duméril et al. (1870–1909), Burt (1935), Coe and Kunkel (1904, 1905, 1906), Cope (1900), Gutberlet (2003), Hunt (1983, 1984), Hutchins et al. (2003), Oliver (1955), Richardson (1852 (reproduced in Bettelheim (2006)), Rieppel (1978, 1981), Rivers (1902), Schoenherr (1976), Smith (1946), Smith and Brodie (1982), Smith et al. 1983, Stebbins (1954, 1959, 1972, 2003), Van Denburgh (1897), Webb et al. (1978), and Zim and Smith





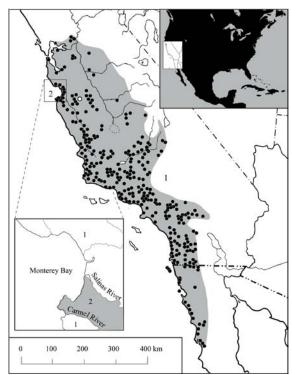
FIGURE 2. Habitat in San Benito County (above) and Los Angeles County (below), California. Photos courtesy of Gary Nafis and CaliforniaHerps.com.

(1956). Black-and-white or color photographs of legless lizards and/or their habitats can be found in Anonymous (2005), Behler and King (1979), Bettelheim (2005), Bezy et al. (1977), Brandes (1974), Cochran and Goin (1970), Dixon (1967), Duellman (1982), Gans (1975), Gevirtz et al. (2007), Grinnell and Grinnell (1907), Grismer (2002), Hill (1948), Hunt (1983), Leviton (n.d.), Mattison (1989), McPeak (2000), Miller (1944), Pianka and Vitt (2003), Pickwell (1947), Powers (1974), Smith (1946), and Van Denburgh (1905, 1922), and Walgren et al. (2005). Gans et al. (1992) illustrated and modeled locomotory behavior of this species in different substrates. Bezy et al. (1977), Gorman (1973), and Matthey (1931b, 1948) illustrated the karyotype. Rieppel et al. (2008) present a 3D high-resolution x-ray computed tomographic reconstruction of the skull.

• **DISTRIBUTION**. This species is widely, though discontinuously, distributed from the confluence of the Sacramento and San Joaquin rivers in Contra Costa County, California southward to the vicinity of Bahia de San Quintin on the Pacific coast of northwestern Baja California Norte, Mexico (see **Comment**). It occurs in a variety of plant communities ranging from coastal dunes near sea level to open pine forest and has been found at elevations up to 2,050 meters in the Sierra Nevada in California and 1,360 meters in the Sierra San Juarez and Sierra San Pedro Martir in Baja California. Populations occur on the desert slopes of the southern Sierra Nevada, Transverse, and Peninsular ranges. Insular populations occur on Islas Los Coronados (north, middle,

and south islands) and Isla Todos Santos (north and south islands) in Baja California Norte, Mexico. *Anniella pulchra* is narrowly sympatric with *Anniella geronimensis* in coastal dunes north and east of Bahia de San Quintin, Baja California Norte, Mexico (Hunt 1983; Shaw 1953).

- FOSSIL RECORD. Although there are numerous fossil localities referable to genus, none of the material found to date can be referred to *Anniella pulchra* (see *Anniella* generic account).
- PERTINENT LITERATURE. The following citations provide information on anatomy and morphology (Bassett 1953; Duméril et al. (1870-1909); Boulenger 1887; Coe and Kunkel 1904, 1905, 1906; Cope 1900; Dufaure and Saint Girons 1984; Eddy 1906; Fischer 1885; Fisher 1934; Gray 1852; Gundy and Wurst 1976; Hamilton 1964; Hunsaker and Johnson 1959; Hunt 1983; Miller 1943; Mosauer 1932; Pough 1969; Richardson 1852; Rieppel 1978, 1981; Senn 1969; Shaw 1940; Smith et al. 1983; Stewart and Daniel 1973; Toerien 1950; Van Denburgh 1905), behavior (Denneen 2002; Gans et al. 1992; Kavanau and Norris 1961; Powers 1974), biogeography (Calsbeek et al. 2003; Cope 1896; Grismer 1993, 1994a,b,c, 2002; Grismer and Mellink 2005; Johnson 1978; Morafka and Banta 1972; Murphy 1983; Olalla-Tárraga et al. 2006; Peabody and Savage 1958; Savage 1960, 1967; Schoenherr 1976; Welsh 1988; Wilcox 1980; Yanev 1980), conservation (Anonymous 2005; Block and Morrison 2005; Block et al. 1988; Brode and Bury 1984; Bury 1972, 1985; Brandes 1974; Bury 2006; California Department of



MAP. Distribution of Anniella pulchra. The circle indicates the restricted type-locality, and dots indicate other records.

Fish and Game 2006; California Department of Parks and Recreation 2004; CDWR and SMPEDT 1999; Center for Biological Diversity 2002; City of Lompoc 2004; Court et al. 2000; Crawford, Multari & Clark Assoc. 2004; Dudek and Assoc. 2003; Dugas et al. 2001: East Bay Regional Park District 2007: Edwards and Pisani 1976; Gevirtz et al. 2007; Graber 1996; Groombridge 1983; Honegger 1979; Hunt and Zander 1997; Jennings and Hayes 1994; Jones & Stokes 2006; Morey 1998; Owens 2001; Rutherford and Rorabaugh 1995; Tempel et al. 2005; Thorne et al. 2002; USDI 2007; USFWS 1995, 1998; Walgren et al. 2005; WRA 2006), ecology, distribution, and natural history (ABA Consultants and Ruth 1998; ABA Consultants and Kuhnz 2000; Banta and Morafka 1968; Barrett et al. 2003; Bernard and Brown 1977; Bettelheim 2005; Bettelheim and Thayer 2006; Block et al. 1998; Bogert 1930; Bogert and Cowles 1947; Bostic 1975; Brattstrom 1965; Brehme 2003; Breininger 1989; Burt 1931; Bury 1983; Bury and Balgooyen 1976; Cope 1883[1884]; Cornett 1979; Crawford 1958; Cunningham 1959; Ditmars 1936; Dixon 1967; Fisher and Case 2000; Fusari 1997; Germano and Morafka 1996; Glaser 1970, Gorman 1957; Gregory 1980; Grinnell and Camp 1917; Grinnell and Grinnell 1907; Grismer 1993, 2001, 2002; Hanley 1943; Hathaway 2000; Henson and Usner 1993; Hill 1948; Hunt 1983, 1997; Jennings and Hayes 1994; Klauber 1924, 1929, 1932, 1934, 1939, 1940; Kuhnz 2000a,b; Kuhnz et al. 2005; Lawrence 1966; Leviton n.d.; Linsdale 1932; Meek 1905; Miller 1943, 1944; Morafka and Banta 1976; Morey 1988; Morrison 1998; Mosauer 1935; Mullen 1989; Murray 1955; Musgrave 1930; Natural Resources Defense Council 2002; Oliver 1955; Parker et al. 2001; Peralta-García et al. 2007: Pianka 1989: Pianka and Vitt 2003: Ramirez 1995; Rivers 1902; Sanders 1950; Schmidt 1922; Schoenherr 1976; Shaw 1953; Slevin 1934; Sprackland 1995, 1996; Stephens 1921; Stoops and Wright 1993; Tietje and Vreeland 1997; Tietje et al. 1997; Van Denburgh 1895, 1897, 1922; Van Denburgh and Slevin 1914, 1921; von Bloeker 1942; Vreeland and Tietje 2000; Zweifel 1952, 1958), field guides, checklists, and keys (Baird and Girard 1853; Banks et al. 1987; Banta and Morafka 1966, 1968; Behler and King 1979; Burg 2007; Burt 1935; Cochran and Goin 1970; Collins 1990; Collins and Taggart 2002; Cope 1875; Crother et al. 2000, 2003; Edwards 1929; Flores-Villela 1993; Frank and Ramus 1995; Garman 1884; Grismer 2001; Hole 1990; Jennings 2004; Liner 1994, 2007; Loomis et al. 1974; McPeak 2000; Nelson 1922; Pickwell 1947; Powell et al. 1998; Pregill and Berriam 1984; Roberts et al. 1980; Rodriguez-Robles et al. 2003; Savage 1952; Schmidt 1953, 1954; Shaw 1950; Slavens and Slavens 1998; Smith 1946; Smith and Brodie 1982; Smith and Smith 1976; Smith and Taylor 1950a,b; Stebbins 1954, 1959, 1966b, 1972, 2003; Stejneger and Barbour 1943; Webb et al. 1978; Werner 2004; Woods 1982; Yarrow 1882; Zim and Smith 1956), genetic variation (Bertolotto et al. 2004; Bezy and Wright 1971; Bezy et al. 1977; Conroy et al. 2005; Gorman and Renzi 1979; Gorman et al. 1971; Gutt-

man 1971; Matthey 1931a,b, 1948; Olmo 2005; Pearse 1996; Pearse and Pogson 2000; Rainey 1984; Rogers et al. 1996; Rosenblum et al. 2004; Schulte et al. 2003), morphological variation (Miller 1943; Hunt 1984; Van Denburgh 1905, 1922), nomenclature (Ballinger et al. 1992; Hunt 1983; Jennings et al. 1992; International Commission on Zoological Nomenclature 1993; Murphy and Smith 1985, 1991), parasites (Adamson 1981; Della Santa 1956; Mc-Allister et al. 1985; Read and Amrein 1952; Stunkard and Lynch 1944; Telford 1965, 1970; Voge and Fox 1950; Walton 1941; Wood 1935), physiology (Bogert and Cowles 1947; Chew 1961; Fusari 1982, 1983, 1984, 1985; Hunsaker and Johnson 1959; Kamel and Gatten 1983), population density (Block and Morrison 1998; Kuhnz et al. 2005; Turner 1977), predation (Bell and Bowden 1995; Cook 1930; Fisher 1901; Gander 1931; Greene 1973; Klauber 1932; Kuhns 1961; Kuhnz et al. 2005; Lowe 1948; Rodriguez-Robles et al. 1999), reproduction (Fitch 1970, 1981; Goldberg and Miller 1985; Miller 1944; Oliver 1955; Porter 1972; Vitt and Price 1982).

 NOMENCLATURAL HISTORY. When John Edward Gray named Anniella pulchra he did not designate a holotype, and did not illustrate or provide a detailed description of the specimen upon which he based his account, saying only that it "will be figured in the forthcoming work on the Zoology of that Voyage." (Gray 1852, p. 437), i.e., the voyage of H.M.S. Herald. Richardson (1852) described and illustrated a specimen of Anniella collected on the same voyage (see reproduction in Bettelheim 2006). Boulenger (1885) provided additional details on the specimen described by Gray in 1852 and Richardson in 1852, but it is evident from the measurements given by Boulenger and Richardson that they were not describing the same individual. The measurements given in Boulenger (1885) match those of the holotype of Anniella pulchra in the British Museum (Hunt 1983). Richardson's specimen has apparently been lost. The holotype of Anniella pulchra in the British Museum, and presumably the one upon which Gray based his original description, actually belongs to the species currently called Anniella geronimensis Shaw 1940. Hunt (1983) speculated that H.M.S. Herald put ashore in Baja California Norte, Mexico, in a localized area around Bahia de San Quintin where these two species are sympatric and that the ship's surgeon, J.O. Goodridge, collected individuals of both species. Differences between the specimens were apparently not noticed until Hunt (1983) re-examined and described the holotype of Anniella pulchra Gray 1852. He considered Anniella geronimensis Shaw 1940 to be a junior objective synonym of Anniella pulchra Gray 1852, applied the name Anniella pulchra to the taxon restricted to Baja California Norte, Mexico, and resurrected the next available name, Anniella nigra Fischer 1885, for the wide-ranging species found in California and Baja California Norte. Murphy and Smith (1985, 1991), Jennings et al. (1992), and Ballinger et al. (1992) disputed this arrangement on the grounds that it destabilized an entrenched nomenclature. The International Commission on Zoological Nomenclature agreed and ruled that all previous fixations of type specimens for the nominate species, *Anniella pulchra*, be set aside and that the holotype of *Anniella nigra argentea* Hunt 1983 be designated the neotype of *Anniella pulchra* Gray 1852 (International Commission on Zoological Nomenclature 1993).

 REMARKS. The distribution and habitat relationships of this unusual lizard have intrigued many workers because of its fossorial habitats and dependence on a narrow range of soil textures, temperatures, and moisture conditions (Miller 1944, Hunt 1997). Although both "subspecies" have regulatory protection (California Department of Fish and Game 2006), this lizard may well be the most common vertebrate in certain habitats. Population densities in excess of 2.282 lizards/hectare (924 lizards/acre) have been documented in coastal dunes in Monterey County (Kuhnz et al. 2005) and 700+ lizards/acre have been found in stabilized dunes in northern Santa Barbara County (L. Hunt, pers. obs.). Despite being locally abundant, populations are spatially discontinuous, reflecting the high spatial variability of soil texture and other edaphic variables (Hunt 1997).

Old records from the San Francisco Peninsula (San Francisco and Palo Alto) and Santa Clara Valley (Alum Rock and San Jose) were dismissed by some authors as erroneous, but are likely valid. For example, much of San Francisco is built upon wind-blown sand deposits whose extant counterparts in the Monterey, Santa Maria, and Los Angeles basins (Cooper 1967) continue to support high densities of legless lizards. Rivers (1902) reported that Anniella pulchra ranged northward to Marin County, but gives no source for this information. The American Museum of Natural History has an old record of Anniella nigra from "Redwood Canyon, Marin County", but which is presumably lost. Old topographic maps show a "Redwood Canyon" (now called Redhead Canyon) located a few miles northeast of San Ardo, Monterey County, well within the known geographic range of this species. Regardless, the occurrence of Anniella north of the San Francisco Bay-Sacramento Delta region has not been verified. The Los Angeles County Museum contains a specimen bearing the locality, "22 mi. W of Blanding, Utah", and the holotype of *Anniella texana* Boulenger 1887 was described from "El Paso, Texas." These two records are far outside the known distribution of Anniella and must be considered errors. The elevational limit for *Anniella pulchra pulchra* described in the **Distribution** section and the range limits in the Sierra Nevada shown on the Map are based upon a specimen from Frazier Mountain, Ventura County found in April 2002 at 6,800 feet (R. Hansen, pers. comm.). Old collections and recent sightings from remnant habitats in Contra Costa, Alameda, San Joaquin, Stanislaus, Fresno, Merced, Tulare, Kings, and Kern counties suggest that Anniella historically ranged across the floor of the San Joaquin Valley, probably as isolated populations associated with wind-blown sand dunes and alluvium deposited by the numerous watercourses that drain the eastern

slopes of the Inner Coast Range and western slopes of the Sierra Nevada. Legless lizards have not been found in the Santa Lucia Range of Monterey and San Luis Obispo counties, but whether this reflects the geology (Franciscan Complex) and subsequent isolation of this landform during the Pliocene, or is an artifact, is unknown at this time. The first record of this species from Inyo County is from Nine Mile Canyon on the desert slope of the Sierra Nevada (R. Hansen, pers. comm.). Other records delimiting the geographic range along the edge of the Mojave Desert include the eastern slopes of the Scodie, Piute, and Tehachapi ranges in Kern County. Legless lizards range widely across high elevation joshua tree-juniper woodlands in the western limits of the Mojave Desert (e.g., Antelope Valley, desert slopes of the San Gabriel Mountains and San Bernardino Mountains, San Gorgonio Pass, Little San Bernardino Mountains), but their range in southern Riverside and eastern San Diego counties coincides closely with the Peninsular Range/Sonoran Desert contact zone (e.g., San Jacinto Mountains, Santa Rosa Mountains, and western Anza Borrego State Park). Stebbins (1966a) mapped Anniella pulchra pulchra as occurring east of the Sierra San Pedro Martir in Baja California Norte, Mexico, to the Gulf of California. This range extension apparently originated from a misinterpretation of the localities "San Jose", and "San Salado River Canon, Lower California", as reported by Meek (1905) and later by Van Denburgh (1922) and Klauber (1932), and "near San Felipe", as reported by Gorman (1957). Bury (1983) demonstrated that all of these localities have Pacific Coast analogues at approximately the same latitude, well within the known range of this species. Specimens from the first 2 localities were collected by Edmund Heller in the late 1800's and deposited at the Field Museum of Natural History (Nos. 1077-1078), but these have been lost. The San Diego Natural History Museum has multiple specimens from the latter locality.

- ETYMOLOGY. The name *pulchra* is the feminine declension of the Latin adjective 'pulcher', meaning beautiful, probably referring to the smooth, shiny scalation and bright dorsal and ventral colors of the nominate taxon. The name *nigra* is the feminine declension of the Latin noun 'niger', meaning black, referring to the dorsal color of the melanistic populations found on and around the Monterey Peninsula in Monterey County, California.
- COMMENT. The taxon currently known as *Anniella pulchra* is composed of at least two potential species-level clades whose geographic distributions do not conform to the boundaries of the currently recognized "subspecies". These clades differ in chromosome number (Bezy and Wright 1971, Bezy et al. 1977), allozymes (Rainey 1984), morphology (Hunt 1984), and mitochondrial DNA sequences (Pearse and Pogson 2000). The "subspecies" *nigra*, was described on the basis of the dark dorsal coloration and relatively shorter tail found in populations of lizards inhabiting coastal dunes fringing the Monterey Pe-

ninsula and southeastern edge of Monterey Bay in Monterey County, California (Cope 1900, Van Denburgh 1905, Grinnell and Camp 1917). Miller (1943, 1944) described "intergrades" between pulchra and nigra in the vicinity of the Monterey Bay north of the Salinas River, However, morphological characters used to define these "subspecies" overlap substantially, and the melanistic dorsal color characteristic of nigra also is found in populations from coastal and interior dunes in the Santa Maria and Los Angeles basins (Grinnell and Camp 1917, Hunt 1984; Figure 3). These northern and southern melanistic populations do not form monophyletic groups with the Monterev Peninsula dark morphs (Pearse and Pogson 2000), and differ in chromosome number (Bezy et al. 1977). Melanism may be an adaptation that allows lizards to thermoregulate more efficiently in cool, fogshrouded coastal habitats (Grinnell and Camp 1917, Miller 1943, 1944, Bury 1985, Pearse and Pogson 2000, Rosenblum et al. 2004), but melanism is not pervasive in coastal populations of this lizard (Hunt 1984). Ongoing mitochondrial DNA analyses (J. Parham and T. Papenfuss, pers. comm.) will likely reveal multiple species-level clades whose phylogeography is closely linked to central and southern California landform evolution on a scale similar to the pattern of differentiation displayed by Batrachoseps salamanders (Yanev 1980, Jockusch and Wake 2002).

1. Anniella pulchra pulchra Gray Silvery Legless Lizard

Anniella pulchra Gray 1852. See species synonymy. Anniella pulchra var. pulchra: Cope 1900:675. Anniella texana: Grinnell and Camp 1917:170. Anniella pulchra pulchra: Grinnell and Camp 1917: 170. First use of trinomial. Anniella nigra argentea Hunt 1983:86.

• **DEFINITION**. Maximum SVL 170 mm, maximum tail length 103 mm, tail length 32%-42% of total length, 86-130 scales along dorsal midline of tail, 24-32 scale rows around mid-body, 16-20 scale rows around anterior portion of tail, 4-8 scale rows between vertebral stripe and first lateral stripe, 1-3 lateral stripes present along sides of body between scale rows, preanal scales usually tipped with brown or black against a more or less clear yellow or whitish-yellow ventral surface. Adult dorsal color varies widely between populations, ranging from dark brownish black, tan, beige, olive-grey, copper, to metallic silver. The ventral surface varies from whitishyellow to bright lemon yellow and is typically unpatterned, but throat and ventral surfaces are heavily pigmented with brownish-grey in southern Sierra Nevada and Tehachapi Mountain populations. A black or brown vertebral stripe, which may be faint or distinct, is typically present. Lateral stripes coalesce on the sides of the head to form an eyestripe in some populations.

2. Anniella pulchra nigra Fischer Black Legless Lizard

Anniella nigra Fischer 1885:9. Type-locality, "S. Diego in California" restricted by Schmidt (1953) to "vicinity of Pacific Grove, Monterey County, California." Holotype, British Museum (Natural History) (BMNH) 86.5.15.41, adult male, collected by J. Behrens, date of collection unknown (examined by author).

Anniella texana Boulenger 1887:52. See species synonymy.

Anniella pulchra var. nigra: Cope 1900:675.

Anniella pulchra nigra: Grinnell and Camp 1917:170. First use of trinomial.

Anniella nigra nigra Hunt 1983:85.

- **DEFINITION**. Maximum SVL 159 mm, maximum tail length 84 mm, tail length 26%–37% of total length, 80–94 scales along vertebral line of tail, 28–34 scale rows around mid-body, 18 scale rows around anterior portion of tail, 4–5 scale rows between the vertebral stripe (when visible) and first lateral line (when visible). The preanal scales are usually tipped with brown or black against a clear yellow ventral surface. Adult dorsal coloration chocolate brown to jetblack. The juvenile dorsal coloration is olive-grey, beige, tan, or light brown, and darkens with age. Ventral color is pale yellow to bright chrome yellow, and the ventral surface is typically immaculate. A vertebral stripe is visible in brownish individuals, not visible in jet-black individuals.
- ACKNOWLEDGMENTS. I thank R. Hansen, R. Fisher, J. Lemm, and T. Papenfuss for sharing locality records, T. Olson for accessing locality records in the California Natural Diversity Data Base, P. Collins for providing access to the library and resources at the Santa Barbara Museum of Natural History, K. Adler and S. Sweet for reviewing the manuscript, and A.H. Price for bibliographic assistance.

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