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Bell, E.L. and A.H. Price. 1996. Sceloporus occidentalis.

Sceloporus occidentalis Baird and Girard Western Fence Lizard

Sceloporus occidentalis Baird and Girard, 1852:175. Type-locality, "Inhabits California, and probably Oregon," restricted to Benicia, [Solano County,] California by Grinnell and Camp (1917). Syntypes, National Museum of Natural History (USNM) 2838, an adult male, and 2866, a subadult female and a hatchling, collected by Dr. J.S. Newberry during the U.S. Exploring Expedition under the command of Charles Wilkes in 1838-1842 (Girard, 1858; Baird, 1859) (see Comment).

Sceloporus frontalis Baird and Girard, 1852:175. Type-locality, "...Puget Sound [Washington]". Holotype, National Museum of Natural History (USNM) 3072, now lost, collected during the U.S. Exploring Expedition under the command of Charles Wilkes in 1838-1842, collector unknown.

Sceloporus undulatus thayerii: Cope, 1875:49 (part).

Sceloporus consobrinus: Cope, 1875:49 (part).

Sceloporus smaragdinus Cope, in Yarrow, 1875:572. Type, type-locality, collector and date of collection not specified. Cochran (1961) listed four specimens in the National Museum of Natural History (USNM 8612) as syntypes, from Beaver [Beaver County], Utah, Dome Canyon, Utah, Nevada, and an unknown locality, collected by H.C. Yarrow in 1872 (see Comment).

Sceloporus undulatus undulatus: Cope, in Yarrow, 1875:573 (part).

Sceloporus undulatus occidentalis: Yarrow, 1882 (1883):61. Sceloporus undulatus: Cope, 1885:398 (part). Sceloporus undulatus consobrinus: Cope, 1900:377 (part).

- Content. Six subspecies are currently recognized: occidentalis, becki, biseriatus, bocourtii, longipes, and taylori. See Remarks.
- **Definition.** Sceloporus occidentalis is a medium-sized member of the undulatus (Smith, 1939) or horridus (Hall, 1973) species group (see the subspecies accounts for snout-vent lengths, inasmuch as these differ considerably between the two exerges). The following meristic data are from Bell (1954b): dorsal scales (counted along the middorsum between the interparietal scale and an imaginary line across the tail connecting the posterior

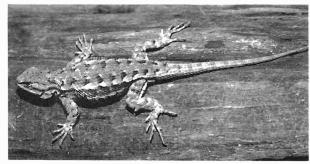
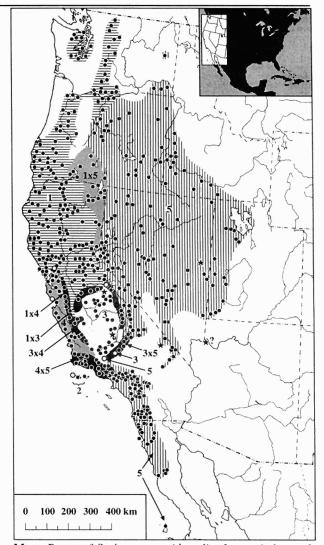


Figure. Adult *Sceloporus occidentalis occidentalis* from the Gifford Pinchot National Forest, Skamania County, Washington (specimen released at site of capture). Photograph by S.L. Collins and J.T. Collins, courtesy of The Center for North American Amphibians and Reptiles.



Map. Range of *Sceloporus occidentalis*. Large circles mark type-localities, dots indicate other records. Note areas of intergradation between subspecies. Stars mark putative fossil localities (see text).

surfaces of the thighs) 35-57 ($\bar{x}=43.16\pm0.06$, SD = 3.18, N = 2930); ventral scales (counted along a midventral line between the postmental scale and the anterior edge of the vent) 60-107 ($\bar{x}=77.67\pm0.12$, SD = 6.72, N = 3165); scales around the mid-body 35-63 ($\bar{x}=46.56\pm0.09$, SD = 4.08, N = 2147); femoral pores 11-23 ($\bar{x}=16.08\pm0.02$, SD = 1.63, N = 5666); medial scales between the femoral pore series 4-20 ($\bar{x}=9.95\pm0.04$, SD = 2.17, N = 3419); fourth toe lamellae 18-31 ($\bar{x}=23.78\pm0.03$, SD = 2.06, N = 4289). The dorsal scales are imbricate and keeled, whereas ventral scales are smooth. A rather sharp line demarcates the larger scales on the upper surface of the rear of the thigh and the smaller scales on the lower surface. The lateral nuchal pocket is lined with small scales. Males have enlarged postanal scales, which are lacking in females.

The dorsal ground color is gray or brown and extends from the head to the base of the tail. The dorsal pattern usually consists of a double row of 5-10 paired spots, transverse bars, or chevron-shaped dark marks edged with green or blue. Such colors are most conspicuous in adult breeding males. These markings are more or less continuous and extend from the dor-

sal midline onto the lower sides across a dorsolateral dark stripe and a lateral light line on each side of the body. The discontinuous lighter dorsolateral stripe is broken into a series of lighter spots which occupy two adjacent half scales, and border the middorsal area from the head onto the tail. A thin dark line originating from the orbit continues posteriorly above the external auditory meatus, then becomes wider as the lateral dark stripe on the lower border of the discontinuous dorsolateral light stripe. The entire dorsum can be quite dark in certain individuals. The posterior surfaces of the fore- and hindlimbs are yellowish to yellow-orange in mature males. Gular semeions (see Smith et al., 1991 for use of this term) in adults are either black (S. o. becki), vestigial or absent (S. o. bocourtii), blue and usually single and paired (S. o. occidentalis), single and transverse across the gular area (S. o. longipes and S. o. biseriatus), or blue and united with the blue of the venter (S. o. taylori) (Bell, 1954a). A distinctively striped form, with continuous dorsolateral light stripes, occurs among populations of normally patterned individuals in the Joshua Tree National Monument and elsewhere in San Bernardino County, California, and in Baja California del Norte, Mexico (Banta, 1963).

- **Descriptions.** Descriptions are in Bell (1954a, b), Camp (1916), Cole (1983), Smith (1946), Stebbins (1954, 1972, 1985), and Van Denburgh (1922). Polymorphism of the gular semeion has been noted by White (1975). The karyotype (2N = 22, with 12 macrochromosomes and 10 microchromosomes) has been described by Cole (1972, 1983), Cole et al. (1967), Jackson and Hunsacker (1969a, b, 1970), and Lowe et al. (1966).
- Illustrations. Basey (1976), Bezy (1991), and Obst et al. (1988) provided color photographs, and color illustrations were provided by Stebbins (1966, 1972, 1985). Black and white photographs were provided by Banta (1963), Breen (1974), Dixon (1967), Pickwell (1947), Sinervo (1993), Sinervo and Huey (1990), Smith (1946), Stebbins (1960), Van Denburgh (1922), and Werner (1972). Clark (1973b) provided a black and white photograph of an individual with a bifid tail. Brand (1979) provided a black and white photograph of footprints. Engbretson (1992) provided a black and white photograph of the skull. Line drawings are in Bocourt (1874), Hallowell (1859), and Stebbins (1954). The arrangement of scales on the posterior surface of the thigh was illustrated by Linder and Fichter (1977) and Savage (1989). Scanning electron micrographs of scales are in the following: Ruibal (1968), Stewart and Daniel (1973), Burstein et al. (1974), and Cole and Van Devender (1976). Wilhoft and Quay (1961) provided photomicrographs of seminiferous tubules. Black and white photographs of habitat were provided by Lillywhite and North (1974) and Lillywhite et al. (1977). Cole (1972), Cole et al. (1967), and Jackson and Hunsaker (1970) illustrated the karyotype.
- Distribution. Sceloporus occidentalis occurs in the Great Basin of Utah and Nevada northward into eastern Oregon and southwestern Idaho and the Blue Mountains of southeastern Washington. It occurs on the east slopes of the Cascades, in the Columbia River Valley, and the Puget Sound area of Washington (Slater, 1963), but has not been reported in the lowland area between the Columbia River and Puget Sound. A single specimen (MVZ 43439) is known from Cheney, near Spokane, Washington. In Oregon the species occurs in the Willamette Valley and the Columbia River Valley east to the mouth of the Deschutes River, and in the Coast Range from California north to about Coos Bay, but it does not occur in the higher northern Coast Range of Oregon and Washington. South of the Great Basin these lizards occur in the Mojave Desert region only on the higher elevations of the Ord, Providence, and New York mountains,

and the Kingston Range. It extends through the Sierra Nevada, Coast Range, Sacramento and San Joaquin valleys, and Tehachapi Mountains through southern coastal California west of the Mojave Desert into the Sierra San Pedro Martir of Baja California del Norte, Mexico. Insular populations occur on Yerba Buena Island, San Francisco County, California (Banta and Morafka, 1966), the Channel Islands off the southern California coast (Savage, 1967), and Islas Cedros and Todos Santos, Baja California del Norte, Mexico (Grismer, 1989; Grismer and Mellink, 1994). Elevations range from sea level to approximately 3300 m.

- Fossil Record. Pleistocene fossils have been identified from California (Bell and Dundas, 1993; Brattstrom 1953a, b, 1955, 1958; Mead et al., 1985) and Nevada (Mead et al., 1983). Other Pleistocene or Holocene fossils, identified as either *Sceloporus occidentalis* or *S. undulatus*, have been reported from Arizona (Mead and Phillips, 1981; Van Devender et al., 1977) and Nevada (Mead et al., 1982, 1989). Mead and Bell (1994) discussed the historical biogeographic context of these fossils.
- Pertinent Literature. Comprehensive references to this species are included in Cope (1900), Fitch (1940a), Gordon (1939), Linder and Fichter (1977), Linsdale (1940), Nussbaum et al. (1983), Smith (1946), Stebbins (1954, 1972, 1985), Van Denburgh (1922), and Woodbury (1931). Systematic and/or phylogenetic studies which have included Sceloporus occidentalis are by Arnold (1995), Cole (1972, 1983), Garland (1994), Guillette et al. (1980), Hall (1973), Larsen and Tanner (1974, 1975), Martins (1994), Reeder (1995), Savage (1958), Sites et al. (1992), Smith (1939), and Wiens (1993). Additional biochemical data were included in Guttman (1970), Mindell et al. (1989), Olmo (1981, 1984), Porter et al. (1994), Sites and Murphy (1991), Wurzinger and Hartenstein (1974), and Wyles and Gorman (1978). Biogeography is discussed by Banta (1962a, b), Bury (1970), Grismer (1993, 1994a, b), Savage (1960, 1967), and Welsh (1988). Liner (1994) listed English and Spanish common names for Mexican forms, but Liner (1996) deleted S. o. biseriatus as not being a member of the Mexican herpetofauna.

Comprehensive ecological studies of Sceloporus occidentalis have included Fitch (1940a), and Tanner and Hopkin (1972). Grover (1996) examined microhabitat use and thermoregulation in a population sympatric with S. undulatus. Clark et al. (1995) reported on pesticide contamination. Further ecological data can be found in Adolph (1990b), Allred et al. (1963), Atsatt (1913), Banta (1957), Banta and Morafka (1968), Block et al. (1988), Coulombe and Banta (1964), Cunningham (1955), Davis and Ford (1983), Davis and Verbeek (1972), Eakin (1957), Ferguson (1952), Fitch (1936), Fuentes (1976), Germano and Lawhead (1986), Gray and Stroud (1980), Hawken (1951), Jaksic and Greene (1984), Johnson et al. (1948), Kahn (1960), Lillywhite and North (1974), Lillywhite et al. (1977), Marcellini and Mackey (1970), Maser et al. (1979), McGinnis (1967), Montanucci (1968), Morafka and Banta (1976), Richardson (1915), Tanner and Jorgensen (1963), Taylor (1912), Van Denburgh and Slevin (1914), Welsh and Lind (1988), and Werschkul (1982). Food habits have been reported by Clark (1973a), Formanowicz and Brodie (1985), Gander (1956), Jameson et al. (1980), Johnson (1965), Jorgensen and Orton (1961), Knowlton (1934, 1937, 1949), Knowlton and Janes (1933, 1934), Knowlton and Nye (1946), Knowlton and Thomas (1934a, b, 1936), Otvos (1977), Rose (1976a, b), Schlesinger et al. (1993), Schonberger (1945), Skehan (1960), Stone (1942), and Whitaker and Maser (1981). Reported predators include mammals (Bond, 1939; Ferrel et al., 1953; Fitch, 1940a; Hawbecker, 1947; Leach and Frazier, 1953; O'Neal, 1933; Sandberg and Banta, 1972[1973]), birds (Balgooyen, 1976; Bryant, 1916; Fitch et al., 1946; Forsman et al., 1984; Grinnell and Linsdale, 1936; Klauber, 1939; Maser et al., 1971; McCurdy, 1983; Steenhof and Kochert, 1985), other lizards (Cunningham, 1956; Fitch, 1940a; Gander, 1931; Shaw, 1950; Skehan, 1960), snakes (Banta and Frantz, 1957; Cunningham, 1959; Fitch, 1936, 1940a, b, 1941; Fitch and Twining, 1946; Hammerson, 1987; Klauber, 1972; McGurty, 1988; Nelson, 1950; Nesbit, 1936; Tanner and Hopkin, 1972), and a salamander, *Dicamptodon ensatus* (Bury, 1972).

Studies of reproductive behavior and physiology have included the following: courtship (Carpenter, 1978; Purdue and Carpenter, 1972a, b; Wood, 1936a); oviposition (Banta and Morafka, 1968; Davis, 1980; LaPointe, 1964; Wood, 1936b); ovarian cycle (Goldberg, 1973, 1974, 1975; Jameson and Allison, 1976); ovarian hypertrophy (Jones et al., 1977); and egg and clutch sizes (Fitch, 1985; Shaw, 1952; Sinervo, 1990a; Storm and Pimental, 1949; Vitt, 1977).

Social behavior has been studied by Duvall (1979, 1981, 1982), Duvall et al. (1987), Hager (1994), and Tarr (1975, 1977a, b, 1979, 1982). Circadian rhythms have been studied by Underwood (1979, 1981, 1983, 1985, 1986), and Underwood and Harless (1985). General learning studies have included Brattstrom (1978) and Gleeson (1979). Chemoreception was reviewed by Simon (1983), who included some new data on this species. Predator avoidance behavior was reported by Johnson (1970). Ejection of blood from the eyes was recorded by Klauber (1939). Studies of locomotor performance have included those by Garland et al. (1990), Marsh and Bennett (1986b), Sinervo and Losos (1991), Sinervo et al. (1991), Tsuji et al. (1989), van Berkum (1988), van Berkum and Tsuji (1987), and van Berkum et al. (1989).

The extensive physiological literature involving Sceloporus occidentalis has included: color change (Atsatt, 1939; Cooper and Ferguson, 1973; Kimball and Erpino, 1971); digestion (Yousef et al., 1977); electrocardiography (Mullen, 1962, 1967; Yackzan et al., 1972); energetics (Bartlett, 1976; Bartlett and Gates, 1967; Bennett, 1980; Bennett and Gleeson, 1976; Bennett and Nagy, 1977; Garland, 1994; Garrick, 1972; Gleeson, 1979, 1982; Lowe et al., 1971; Mueller, 1970a, b; Pough, 1973; Tsuji, 1988a, b); glutathione peroxidase (Tappel et al., 1982); growth (Gehrmann et al., 1991); hormones (Erpino, 1971; Gorbman, 1939, 1946; Licht, 1970; Quay and Wilhoft, 1964; Quay et al., 1970; Wilhoft and Quay, 1965); muscle physiology (Adams, 1987; Marsh and Bennett, 1986a, b; Putnam and Bennett, 1982), respiration (Bennett and Ruben, 1975; Dawson and Poulson, 1962; Heusner and Jameson, 1981; Jameson et al., 1977; Mazzarella, 1976; Munsey, 1972; Pough, 1969a, 1976; Snyder and Weathers, 1977; Vinegar and Hillyard, 1972; Weathers and White, 1972); stress (Dunlap, 1995a, b; Dunlap and Wingfield, 1995); thermoregulation (Adolph, 1990a; Bakken and Gates, 1975; Brattstrom, 1965; Cowgell and Underwood, 1979; Cunningham, 1966a, b; Engbretson and Livezey, 1972; Harwood, 1979; Kour and Hutchison, 1970; Larson, 1961; Lashbrook and Livezey, 1970; Linsdale, 1938; McGinnis, 1966, 1970; Porter, 1967; Sinervo, 1990b; Sinervo and Adolph, 1989, 1994; van Berkum, 1988; Vitt, 1974; Wang and Adolph, 1995; Whitfield and Livezey, 1973; Wilhoft and Anderson, 1960); and thyroid physiology (Chiu et al., 1970; John-Alder, 1990; Kobayashi and Gorbman, 1959; Sinervo and Dunlap, 1995; Stebbins and Tong, 1973).

Anatomical studies have included the following: nasal structure (Stebbins, 1948); dentition (Olson et al., 1986); hemipenes (Böhme, 1988); liver and gall bladder (Ells, 1954); effect of temperature on thyroid histology (Wilhoft, 1958); testicular histology (Wilhoft and Quay, 1961); skeleton (Etheridge, 1964, 1965; Frazzetta, 1962); choroid plexus and paraphysis

(Shuangshoti and Netsky, 1966); hypophysis (Saint Girons, 1967); digestive tract (Johnson et al., 1967; Parsons and Cameron, 1977); cutaneous innervation (Miller and Kasahara, 1967); morphological adaptation to undersand respiration (Pough, 1969b); cloacal gland (Burkholder and Tanner, 1974); ovary (Jones et al., 1977, 1982); scleral ossicles (de Queiroz, 1982); taste buds (Schwenk, 1985); hermaphroditism (Goldberg, 1989a); orchitis (Goldberg, 1989b); femoral glands (Alberts, 1991). The relationship of body size and a number of life-history parameters have been studied by Davis (1967), Dawson and Bartholomew (1956), Fitch (1978), Halliday and Verrell (1988), Pough (1977), Sinervo (1993), Sinervo and Huey (1990), and Turner et al. (1969).

Considerable research has been done on the parietal eyepineal gland complex by Bethea and Walker (1978), Bickler and Nagy (1980), Eakin (1964a, b, 1968, 1970, 1973), Eakin and Stebbins (1959), Eakin and Westfall (1959, 1960), Eakin et al. (1959, 1961), Francis and Brooks (1970), Gundy and Wurst (1976), Quay (1971), Quay et al. (1971), Stebbins (1960), Stebbins and Cohen (1973), and Stebbins and Eakin (1958). Studies on other sense organs have included the following: eye (Bernstein et al., 1984; Farber et al., 1981; Williams et al., 1986; Young, 1977); ear (Miller, 1966, 1975, 1978, 1981; Werner, 1972; Wever, 1978); integumentary system (Atsatt, 1939; Coleman and Livezey, 1968; Hunsacker and Johnson, 1959; Norris, 1967; and Talbot and Livezey, 1964).

Parasitism has been studied extensively in this species. Comprehensive studies include those by Telford (1970) and Wood (1935). Salmonella was reported by Burdick et al. (1984) and Hinshaw and McNeil (1947). Studies of the malarial parasite Plasmodium mexicanum in this lizard have included Ayala (1970b, 1971, 1973, 1978), Ayala and Lee (1970), Bromwich and Schall (1986), Jordan (1970), Klein et al. (1987, 1988), Moore and Sinden (1974), Schall (1989), and Wood and Wood (1936). Dunlap and Mathies (1993), Dunlap and Schall (1995), Ressel and Schall (1989), Schall (1983a, b, 1990), Schall and Dearing (1987), Schall and Houle (1992), Schall and Sarni (1987), and Schall et al. (1982) studied host fitness effects of malarial infection. Lefcort and Blaustein (1991) included S. occidentalis in a study relating parasite load and fitness. Infections by other sporozoans are reported by Ayala (1970a, c), Ball (1944), Bonorris and Ball (1955), Bovee and Telford (1965), Clark (1970), Clark and Bradford (1969), Clark and Colwell (1973), Oda et al. (1971), Sinden and Moore (1974), and Telford (1966). Nematode parasitism was reported by Gambino (1957, 1958), Gambino and Heyneman (1960), Goldberg and Bursey (1988), Grundmann (1959), Lyon (1986), Pearce and Tanner (1973), Telford (1965, 1970), Waitz (1961), and White and Knapp (1979). Ryckman (1954) reported that lizards were refractory to infection by Trypanosoma cruzi after eating infected Triatoma. Cestode infection has been reported by Goldberg and Bursey (1990), Lyon (1986), Mankau and Widmer (1977), Pearce and Tanner (1973), Specht and Voge (1965), Voge (1953), Voge and Fox (1950), and White and Knapp (1979). Ticks and mites have been reported on S. occidentalis by Allred and Beck (1962), Arthur and Snow (1968), Ashcraft (1937), Bishopp and Trembley (1945), Brennan (1948), Brennan and Jones (1954), Burrage (1966), Cooley and Kohls (1945), Jameson (1972), Jellison (1934), Klauber (1939), Mohr et al. (1964), Powder and Loomis (1962), and Reichenbach-Klinke and Elkin (1965). Kimsey and Kimsey (1984) used rubidium to detect the feeding of blood-sucking arthropods. Plasma antibodies against the tickborne spirochaete Borellia burgdorferi, the causative agent of Lyme disease, have been detected in some specimens of S. occidentalis in northern California (Lane, 1990; Lane and Loye, 1989; Manweiler et al., 1990, 1992), although the spirochaete itself has not been recovered.

- Nomenclatural History. Following various government expeditions exploring the American West, the taxonomic relationships between the two widespread polytypic species Sceloporus occidentalis and S. undulatus were much confused. At least five new species were described from specimens taken from throughout the range of the former. These taxa were considered conspecific to varying degrees by subsequent workers (e.g. Bocourt, 1874; Boulenger, 1885, 1897; Cope, 1875, 1883 [1884], 1885, 1900; Cope in Yarrow, 1875; Yarrow, 1882 [1883]) in a bewildering array of nomenclatural combinations. Camp (1916) was the first to clearly recognize the infraspecific relationships within S. occidentalis, followed by Grinnell and Camp (1917) who designated four subspecies: occidentalis, becki, biseriatus, and taylori. These developments were ignored by Burt (1933, 1935), who persisted in following the earlier placement of S. occidentalis within a single transcontinental species, S. undulatus. Smith (1938, 1939) reiterated the distinctness of the two forms at the species level, but Shannon (1950) suggested that S. occidentalis might intergrade with S. u. tristichus in the vicinity of Lake Meade. Both Bell (1954a), by studying museum specimens, and Cole (1983), through field work, confirmed sympatry with no intergradation of the two taxa in the Pine Valley Mountains of southwestern Utah. Bell (1954a) recognized six subspecies, adding longipes and bocourtii. The phylogenetic relationships among and taxonomic status of the subspecies of S. occidentalis are badly in need of study.
- Remarks. The six subspecies were arranged in two exerges by Smith et al. (1992): occidentalis and bocourtii in the occidentalis exerge, and becki, biseriatus, longipes, and taylori in the biseriatus exerge. Members of the occidentalis exerge are smaller, with only 4.6% of 847 specimens larger than 60 mm SVL examined exceeding 75 mm SVL. The gular semeions (Smith et al., 1991) are usually divided or vestigial, and the chests, thighs, and interabdominal semeion areas (IASA) are white to cream-colored. Members of the biseriatus exerge are larger, with 48% of 971 specimens larger than 60 mm SVL examined exceeding 75 mm SVL. The larger size of members of the biseriatus exerge is presumably due to a larger egg and yolk sac (Sinervo, 1990a; Sinervo and Huey, 1990). The gular semeion usually is an undivided transverse feature, and chests, thighs, and IASAs are much darker (Smith et al., 1992).
- Etymology. The name *occidentalis* (L., "western") refers to the continental distribution of the species. The name *biseriatus* (L., *bi* = "two" and *seriatus* = "to arrange in series") refers to the two dorsolateral series of light spots in the dorsal pattern of this taxon. The name *longipes* (L., *longus* = "long" and *pes* = "foot") refers to the long toes of this form. The patronyms *bocourtii*, *taylori*, and *becki* honor the French herpetologist Marie-Firmin Bocourt, and the two collectors of the remaining type-specimens, respectively.
- Comment. Baird and Girard (1852) did not list any type-material in their original description of *Sceloporus occidentalis*. Girard (1858) provided a detailed description of one of the specimens, an adult male, without an accompanying museum number. Baird (1859) listed two specimens, USNM 2838 (Benicia, [Solano Co.,] California) and USNM 2866 (Upper Willamette Valley [Clackamas Co., Oregon]) as syntypes; the specimens were still listed as extant by Cope (1900, as *Sceloporus undulatus undulatus*) but not by Cochran (1961). Grinnell and Camp (1917) restricted the type-locality to that of USNM 2838 based on Baird (1859), and Bell (1954a) designated, without comment, another specimen (MVZ 59874) from the same locality as the neotype. According to R.P. Reynolds (in litt., 2.V.1996), USNM 2838 (presumably Girard's male) is lost, but USNM 2866 still

exists and consists of two specimens, both *S. occidentalis*, a subadult female in good condition and a poorly preserved hatchling. With the discovery of these two syntypes, Article 75(h) of the International Code of Zoological Nomenclature requires the International Commission on Zoological Nomenclature to rule on the status of the name-bearing type of *Sceloporus occidentalis*, a process which we have initiated.

The syntypes of *Sceloporus smaragdinus* are all mixed and cannot now be associated with a specific locality (Robert P. Reynolds, in litt., 2.V.1996).

• Acknowledgments. We thank R.P. Reynolds (USNM) and E.V. Malnate (ANSP) for tracking down specimen data and providing ancillary information.

Sceloporus occidentalis occidentalis Baird and Girard Northwestern Fence Lizard

Sceloporus occidentalis Baird and Girard 1852:175. See species synonymy.

Sceloporus frontalis Baird and Girard 1852:175. See species synonymy.

Sceloporus consobrinus: Cope, 1875:49 (part). See species synonymy.

Sceloporus undulatus undulatus: Cope, in Yarrow, 1875:573 (part). See species synonymy.

Sceloporus undulatus thayeri: Yarrow, 1882 [1883]:60 (part). Sceloporus undulatus occidentalis: Yarrow, 1882 [1883]:61. See species synonymy.

Sceloporus undulatus consobrinus: Cope, 1900:377 (part). See species synonymy.

Sceloporus occidentalis occidentalis: Camp, 1916:65. First use of combination.

• **Definition.** This sexually monomorphic subspecies is relatively small, with male and female SVLs 55-84 mm ($\bar{x}=65.28\pm0.22$, SD = 4.96, N = 494) and 55-80 mm ($\bar{x}=66.09\pm0.34$, SD = 5.35, N = 248), respectively. Only 34 of 668 (5.1%) adults with SVL > 60 mm examined attained an SVL of 75 mm or more (Smith et al., 1992). Maximum recorded SVLs are 85 mm for a male from Napa County, California, and 89 mm for a female from Shasta County, California. Scalation is as follows (Bell, 1954b): dorsal scales 37-52 ($\bar{x}=42.44\pm0.08$, SD = 2.34, N = 945); ventral scales 60-87 ($\bar{x}=73.55\pm0.15$, SD = 4.72, N = 936); scales around the mid-body 37-53 ($\bar{x}=44.85\pm0.10$, SD = 2.74, N = 739); femoral pores 11-21 ($\bar{x}=15.41\pm0.03$, SD = 1.48, N = 1828); medial scales between the femoral pore series 4-13 ($\bar{x}=9.06\pm0.05$, SD = 1.43, N = 916); fourth toe lamellae 19-29 ($\bar{x}=22.73\pm0.04$, SD = 1.68, N = 1558).

The dorsal ground color is grayish, brownish, or olive, with a series of crescent-shaped brownish spots between the middorsal line and interrupted dorsolateral light lines. A dark lateral line lies below the dorsolateral light line and above a lateral light line, which extends between the limb insertions. Dorsal spots may or may not be connected by thin lines across the dorsolateral light lines to spots of the lateral dark line. Dorsal scales often have bluish or greenish edges, particularly in males. Posterior ventral surfaces of the limbs are yellowish around the femoral pores. The IASA are light or white, bordered medially by black, and almost always lighter than those of members of the biseriatus exerge. Ventral coloration is less intense in females.

• Diagnosis. This subspecies can be distinguished from members of the *biseriatus* exerge by its smaller size, and from all other subspecies by the possession of lateral, prominent, and distinctly separate blue gular semeions, or a large blue gular semeion divided by a single row of medial light scales. The

chest, chin, and IASA are light-colored, often white. Five or more gular semeion scales are at least 50% blue in females, whereas at least 20 such scales are present in males.

2. Sceloporus occidentalis becki Van Denburgh Island Fence Lizard

Sceloporus becki Van Denburgh, 1905:9. Type-locality, "San Miguel Island, [Santa Barbara County,] California." Holotype, California Academy of Sciences (CAS) 4357, an adult male, collected by R.H. Beck on 26 March 1903 (examined by senior author).

Sceloporus biseriatus becki: Van Denburgh, 1905:11. First use of trinomial.

Sceloporus occidentalis becki: Grinnell and Camp, 1917:162. First use of combination.

Sceloporus undulatus becki: Burt, 1935:281.

• **Definition.** This sexually monomorphic subspecies is of medium size, 55-80 mm SVL ($\bar{x}=66.15\pm0.73$, SD = 6.16, N = 71, both sexes combined). Eight of 59 (13.5%) adults larger than 60 mm SVL examined attained an SVL of 75 mm or more. Maximum recorded SVLs are 80 mm (male) and 75 mm (female), both from Santa Cruz Island, California (Bell, 1954b); Smith et al., 1992). Scalation is as follows (Bell, 1954b): dorsal scales 43-52 ($\bar{x}=47.25\pm0.18$, SD = 1.68, N = 87); ventral scales 75-90 ($\bar{x}=82.79\pm0.38$, SD = 3.47, N = 84); scales around midbody 47-57 ($\bar{x}=50.72\pm0.21$, SD = 1.91, N = 82); femoral pores 14-20 ($\bar{x}=16.64\pm0.08$, SD = 1.10, N = 171); medial scales between the femoral pore series 8-17 ($\bar{x}=11.59\pm0.17$, SD = 1.61, N = 87); fourth toe lamellae 19-29 ($\bar{x}=24.94\pm0.14$, SD = 1.73, N = 148).

A paired series of poorly defined dark brown dorsolateral blotches on the dorsum border a well defined dorsolateral longitudinal light stripe 1.5-3 scales wide, extending from above the ear opening onto the base of the tail. Another poorly defined series of dark brown blotches composes the lateral dark stripe just below the longitudinal light stripe. The middorsal area is grayish or brownish with many greenish blue scales, particularly in males. Mature males possess conspicuous blue abdominal semeions bordered medially by black. The interabdominal semeion area is dark, but not as black as the borders of the abdominal semeions. A yellowish band is present along the femoral pores on the posterior edge of the thigh.

- **Diagnosis.** This subspecies can be distinguished from members of the *occidentalis* exerge by its relatively larger size, and from all other subspecies by the large undivided blackish medial gular semeion with black lines radiating forward to the edges of the chin, with pale blue on the chin between the black lines.
- Remarks. This subspecies inhabits the Channel Islands of Santa Cruz, Santa Rosa, and San Miguel; all are emergent peaks of the Santa Monica Mountains (Weaver and Doerner, 1967).

Van Denburgh (1905) indicated a unique feature of *S. becki* was contact of the supraoculars with the frontoparietals. Bell (1954b), however, found only 8 of 87 (9.2%) specimens from Santa Rosa and Santa Cruz islands with this feature. A re-examination of the specimens used by Van Denburgh (1905) is not possible, as all but the type were destroyed in the San Francisco earthquake and fire of 1906.

3. Sceloporus occidentalis biseriatus Hallowell San Joaquin Fence Lizard

Sceloporus bi-seriatus Hallowell, 1854:93. Type-locality, "borders of El Paso Creek and in Tejon Valley [Kern County,

California]", restricted by Smith and Taylor (1950a, b) to the borders of El Paso Creek. This creek is about 10 mi (16 km) northeast of Fort Tejon. Lectotype, designated by Bell (1954a), Academy of Natural Sciences of Philadelphia (ANSP) 8476, an adult female, collected by Dr. Heermann, date of collection unknown (examined by senior author).

Sceloporus bi-seriatus var. A. azureus Hallowell, 1854:94. Typelocality, "borders of El Paso Creek and in Tejon Valley [Kem County, California]" (by inference), restricted by Bell (1954a) to El Paso Creek. Syntypes (Malnate, 1971), Academy of Natural Sciences of Philadelphia (ANSP) 8477-9, two adult males and an adult female, collected by Dr. Heermann, date of collection unknown (not examined by authors).

Sceloporus bi-seriatus var. B. variegatus Hallowell, 1854:94.
Type-locality, "borders of El Paso Creek and in Tejon Valley [Kern County, California]" (by inference), restricted by Bell (1954a) to El Paso Creek. Holotype not designated, collected by Dr. Heermann, date of collection unknown.

Sceloporus undulatus thayeri: Yarrow, 1882 (1883):60 (part). Sceloporus biseriatus: Cope, 1885:398 (part).

Sceloporus occidentalis bi-seriatus: Camp 1916:65 (part). First use of combination.

Sceloporus undulatus bi-seriatus: Burt, 1933:238 (part).

• **Definition.** This sexually dimorphic subspecies is relatively large, with male and female SVLs of 55-93 mm (\bar{x} = 74.70 \pm 0.76, SD = 8.04, N = 112) and 56-87 mm (\bar{x} = 69.36 \pm 0.89, SD = 7.09, N = 64), respectively. Eighty-nine of 171 (52%) adults larger than 60 mm SVL examined attained an SVL of 75 mm or more. Maximum recorded SVLs are 93 mm (male) and 95 mm (female), from Tulare and Kern counties, California, respectively (Smith et al., 1992). Scalation is as follows (Bell, 1954b): dorsal scales 43-57 (\bar{x} = 48.47 \pm 0.17, SD = 2.47, N = 203); ventral scales 80-107 (\bar{x} = 91.74 \pm 0.34, SD = 4.82, N = 200); scales around mid-body 47-63 (\bar{x} = 54.36 \pm 0.29, SD = 3.45, N = 140); femoral pores 13-23 (\bar{x} = 17.80 \pm 0.08, SD = 1.52, N = 393); medial scales between femoral pore series 9-20 (\bar{x} = 14.60 \pm 0.15, SD = 2.07, N = 199); fourth toe lamellae 20-29 (\bar{x} = 25.53 \pm 0.09, SD = 1.50, N = 290).

The dorsal and ventral coloration is much like that found in *S. o. longipes*, except that the blue gular semeion sometimes, but not often, has three or four fine light spots. Conspicuously striped individuals are absent.

- **Diagnosis.** This subspecies can be distinguished from members of the *occidentalis* exerge by its relatively larger size, and from all other subspecies except *longipes* and immature *taylori* by the occurrence in adult males of a large single blue gular semeion without radiating dark lines, which occasionally is indented or divided, and a dark gray to black chest, ventral surface of thighs, and IASAs. It can be distinguished from *longipes* by relatively higher dorsal and ventral scale counts.
- Remarks. Hallowell (1859) provided an expanded version of his original description of *Sceloporus biseriatus*. Strecker (1929) commented on a transcription error of the type-locality by Stejneger and Barbour (1923).
- Comment. This subspecies occurs in the San Joaquin Valley and Sierra Nevada of California from Fresno County south to the Tehachapi Mountains in Kern County. It appears to be absent from a xeric region in the San Joaquin Valley southwest of Bakersfield, and intergrades with S. o. taylori at elevations around 2,134 m in the Sierra Nevada.

4. Sceloporus occidentalis bocourtii Boulenger Coast Range Fence Lizard

Sceloporus biseriatus: Bocourt, 1874:197 (part).

Sceloporus undulatus var. bocourtii Boulenger, 1885:229. Typelocality not specified, restricted to Santa Cruz, Santa Cruz County, California by Bell (1954a). Holotype not specified; lectotype, British Museum of Natural History (BMNH) 1946-9-6, 98 (Bell, 1954a), an adult male, collector and date of collection unknown (examined by senior author).

Sceloporus occidentalis bocourti: Bell, 1954a:35. First use of combination.

• **Definition.** This sexually dimorphic subspecies is relatively small, with male and female SVLs 50-76 mm ($\bar{x} = 64.61 \pm 0.55$, SD = 6.16, N = 124) and 51-79 mm ($\bar{x} = 67.80 \pm 0.66$, SD = 10.665.11, N = 60), respectively. Only five of 179 (2.8%) adults larger than 60 mm SVL examined attained an SVL of 75 mm or more (Smith et al., 1992). Maximum recorded SVLs are 82 mm for a male from Santa Barbara County, California, and 79 mm for two females from Alameda and Santa Barbara counties, California (Smith et al., 1992). Scalation is as follows (Bell, 1954b): dorsal scales 37-49 ($\bar{x} = 42.40 \pm 0.12$, SD = 2.11, N = 331); ventral scales 62-88 ($\bar{x} = 74.19 \pm 0.23$, SD = 4.15, N = 322); scales around midbody 39-53 ($\bar{x} = 44.71 \pm 0.16$, SD = 2.33, N = 212); femoral pores 12-22 ($\bar{x} = 15.76 \pm 0.05$, SD = 1.37, N = 627); medial scales between the femoral pore series 5-13 (\bar{x} = 8.97 ± 0.08 , SD = 1.40, N = 316); fourth toe lamellae 18-28 (\bar{x} $= 22.68 \pm 0.10$, SD = 1.88, N = 382).

The dorsal ground color is brown or grey. The dorsolateral dark line originates as a thin line extending posteriorly from the canthus rostralis above the ear opening and continues as a series of enlarged dark brown spots which extend onto the base of the tail. Another series of dark spots extend laterally between the limb insertions, and may or may not be connected with the dorsolateral series by thin dark lines extending across an intervening series of light spots 1-2 scales wide. The neck, chest, and gular region are gray to white with a few dark flecks, and the IASA are white or light-colored with only a few dark flecks. Conspicuous abdominal blue semeions are 1-3 scales wide and are bordered by distinct (males) or less distinct (females) medial black borders. A yellow area (larger in males) extends along the femoral pores on the posterior surface of the thighs.

- **Diagnosis.** This subspecies can be distinguished from members of the *biseriatus* exerge by its smaller size, and from all other subspecies by the virtual absence of blue gular semeions. Gular scales which are at least 50% blue averaged 1.4 (0-16, N = 84) in adult females and 7.4 (0-45, N = 101) in adult males. Of the females examined, 66 (78.5%) had no blue gular scales. Adult males examined generally had fewer than 20 such scales, and in 43 (42.5%) blue gular scales were absent (Bell, 1954b). The chest, chin, and IASA are light-colored, often white.
- Comment. This form occurs in the Coast Range of California from San Francisco and Contra Costa counties southward into San Luis Obispo and Santa Barbara counties.

5. Sceloporus occidentalis longipes Baird Great Basin Fence Lizard

Sceloporus longipes Baird, 1858(1859):254. Type-locality, "Fort Tejon, [Kern County] Cal[ifornia]." Lectotype, National Museum of Natural History (USNM) 4358, an adult male, collected by John Xantus DeVesey, date of collection unknown (examined by senior author) (see Remarks).

Sceloporus nigro-ventris: Bocourt, 1874:199. Sceloporus biseriatus: Cope, 1875:48 (part). Sceloporus smaragdinus Cope, in Yarrow, 1875:572. See species synonymy.

Sceloporus undulatus undulatus: Yarrow, 1882 (1883):59 (part). Sceloporus undulatus thayeri: Yarrow, 1882 (1883):60 (part). Sceloporus consobrinus: Yarrow, 1882 (1883):61 (part). Sceloporus undulatus: Cope, 1885:398 (part). Sceloporus undulatus smaragdinus: Cope, 1885:399. Sceloporus occidentalis bi-seriatus: Camp, 1916:65 (part; by inference).

Sceloporus undulatus bi-seriatus: Burt, 1933:238 (part). Sceloporus undulatus elongatus: Burt, 1933:243 (part). Sceloporus occidentalis longipes: Bell, 1954a:33. First use of combination.

• **Definition.** This subspecies is relatively large. The Great Basin/Columbia River Plateau population is sexually monomorphic, with male and female SVLs 55-91 mm ($\bar{x} = 73.22 \pm 0.47$, SD = 7.66, N = 267) and 55-93 mm ($\bar{x} = 73.96 \pm 0.63$, SD =7.85, N = 156), respectively. The southern coastal California/ Baja California populations are sexually dimorphic, with male and female SVLs 55-85 mm ($\bar{x} = 70.51 \pm 0.76$, SD = 6.76, N = 156) and 57-79 mm ($\bar{x} = 67.00 \pm 0.67$, SD = 5.52, N = 68), respectively. Two hundred seventy-two of 478 (51%) adults larger than 60 mm SVL from the Great Basin examined attained an SVL of 75 mm or more, whereas 69 of 228 (22%) from coastal populations did so. Maximum recorded SVLs are 91 mm (male) and 97 mm (female), from Nevada and San Diego County, California, respectively (Smith et al., 1992). Scalation from the northern portion of the range is as follows (Bell, 1954b; Tanner and Banta, 1966): dorsal scales 35-50 ($\bar{x} = 43.53 \pm 0.10$, SD = 2.26, N = 540); ventral scales 66-88 (\bar{x} = 78.09 ± 0.18, SD = 4.23, N = 539); scales around midbody 35-56 ($\bar{x} = 47.28 \pm 0.14$, SD = 2.94, N = 439); femoral pores 12-22 ($\bar{x} = 16.70 \pm 0.05$, SD = 1.63, N = 1033); medial scales between the femoral pore series 6-16 ($\bar{x} = 9.87 \pm 0.07$, SD = 1.57, N = 517); fourth toe lamellae 19-30 ($\bar{x} = 24.23 \pm 0.06$, SD = 1.76, N = 851). Scalation from the southern portion of the range is as follows (Bell, 1954b): dorsal scales $35-\overline{46}$ ($\bar{x} = 40.65 \pm 0.11$, SD = 2.12, N = 348); ventral scales 69-86 ($\bar{x} = 77.22 \pm 0.18$, SD = 3.40, N = 342); scales around midbody 38-53 ($\bar{x} = 44.80 \pm 0.18$, SD = 2.40, N = 171); femoral pores 12-21 ($\bar{x} = 16.02 \pm 0.05$, SD = 1.31, N = 672); medial scales between the femoral pore series 6-14 (\bar{x} = 9.69 ± 0.08 , SD = 1.42, N = 344); fourth toe lamellae 21-30 (\bar{x} $= 25.34 \pm 0.08$, SD = 1.56, N = 410).

Apparent color pattern differences between the two disjunct populations are inconsistent. The dorsal ground color is brown, olive, or gray. The head is brown or gray, with narrow cross-lines of darker brown. A series of dark blotches or crossbands is present on either side of the midline. These are often connected by narrow lines which cross a lighter dorsolateral line and connect with a lateral dark line. The latter originates as a narrow line at the posterior edge of the eye, becomes wider above the ear opening, and gives rise to a dark spot above the anterior limb insertion. The dorsal scales often have a blue spot, especially in males during the breeding season. The IASA, throat, chin, and chest are dark. The gular area almost always has a wide blue semeion of uniform intensity. The venter has conspicuous blue abdominal semeions bordered medially with black in males; this coloration is less conspicuous in females. A distinctive striped phenotype occurs with normally colored individuals in Joshua Tree National Monument, Riverside and San Bernardino counties, California, and near San José, Baja California. The dorsolateral light stripes are 2-3 scales wide and continuous, and middorsum and lateral body are often quite dark.

- Diagnosis. This subspecies can be distinguished from members of the *occidentalis* exerge by its relatively larger size, and from all other subspecies except *biseriatus* by the occurrence in adult males of a large single blue gular semeion without radiating dark lines, which occasionally is indented or divided, and a dark gray to black chest, ventral surface of thighs, and IASAs. It can be distinguished from *biseriatus* by relatively lower dorsal and ventral scale counts.
- Remarks. Baird (1858 [1859]) did not specify his type-material when he described this taxon. Cochran (1961) listed 25 specimens (USNM 4358) as syntypes, whereas Cope (1900) listed 15 specimens under that number and an additional 10 specimens (USNM 4359) as syntypes. Cope's (1900) breakdown conforms to the original catalogue entries in the National Museum of Natural History (R.P. Reynolds, in litt., 2.V.1996). Bell (1954a) designated one of the original 15 specimens of USNM 4358 as the lectotype, and subsequently one specimen of each series was exchanged with other institutions (Reynolds, op. cit.). By 18 December 1989, 25 specimens, all bearing original metal tags numbered 4358, were extant; all but the lectotype were recatalogued as USNM 292183-292206 (R.P. Reynolds, op. cit.). Eight specimens bearing original metal tags were associated with USNM 4359; the fate of the missing specimen in addition to the one previously exchanged is unknown. The discrepancy between the original ledger entries and the current disposition of USNM 4358 and 4359 remains unresolved.
- Comment. The range of this subspecies is disjunct. The major portion includes the Great Basin, northward onto the Columbia River Plateau into Oregon, Idaho, and extreme southeastern Washington, and southward in the Mojave Desert region only at higher elevations of the Providence Mountains, the New York Mountains, and the Kingston Range. The remainder of the range includes central Los Angeles County, southward along the coast west of the Mojave Desert into the Sierra San Pedro Martir of Baja California, and on Islas Cedros and Todos Santos, Baja California, México. The two areas are connected by a narrow zone of intergradation with biseriatus in the Tehachapi Mountains of Kern County, California.

6. Sceloporus occidentalis taylori Camp Sierra Fence Lizard

Sceloporus occidentalis taylori Camp, 1916:66. Type-locality, "half way between Merced Lake and Sunrise Trail (Echo Creek basin), altitude 7500 feet, Yosemite National Park, [Mariposa County] California". Holotype, Museum of Vertebrate Zoology (MVZ) 5947, an adult male, collected 25 August 1915 by Walter P. Taylor (examined by senior author).

Sceloporus undulatus taylori: Burt, 1935:282.

• **Definition.** This sexually monomorphic subspecies is relatively large, with male and female SVLs of 60-94 mm (\bar{x} = 80.18 ± 1.49, SD = 8.57, N = 33) and 57-84 mm (\bar{x} = 74.10 ± 1.77, SD = 7.90, N = 20), respectively. Twenty-nine of 35 (83%) adults examined larger than 60 mm SVL attained an SVL of 75 mm or more. Maximum recorded SVLs are 94 mm (male) and 84 mm (female), from Tulare and Fresno counties, and Yosemite National Park, California, respectively (Smith et al., 1992). Scalation is as follows (Bell, 1954b): dorsal scales 44-57 (\bar{x} = 48.98 ± 0.28, SD = 2.50, N = 80); ventral scales 79-107 (\bar{x} = 90.38 ± 0.47, SD = 4.24, N = 80); scales around midbody 48-60 (\bar{x} = 53.32 ± 0.30, SD = 2.51, N = 72); femoral pores 14-21 (\bar{x} = 17.21 ± 0.11, SD = 1.40, N = 159); medial scales between the femoral pore series 11-19 (\bar{x} = 13.65 ± 0.18, SD = 1.61, N =

78); fourth toe lamellae 22-29 ($\bar{x} = 25.31 \pm 0.13$, SD = 1.43, N = 129).

The dorsal ground color is brown or gray, marked by blotches or undulate crossbands of dark brown. Dorsal scales are spotted with green or pale blue. A dorsolateral light line may or may not be present in older individuals, and is more evident in adults 80 mm SVL or less.

- **Diagnosis.** Adults of this subspecies may be distinguished from all other subspecies except *biseriatus* by relatively high dorsal and ventral scale counts, and from all other subspecies by their unique ventral coloration. Adults larger than 75 mm SVL show with increasing age extensive blue coloration on the chin, chest, and between the abdominal semeions, with the black borders of the semeions becoming blue, until at about 81 mm SVL in males almost the entire venter from the chin to the posterior abdomen, and the ventral surfaces of the hind limbs, are blue (Basey, 1976).
- Remarks. This subspecies occurs in the higher reaches of the Sierra Nevada above 2,134 m in Tuolumne, Mariposa, Madera, Fresno, and Tulare counties, California (Bell, 1954b; Smith et al., 1992).

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