

A New Species Of *Vaccinium* (Ericaceae) From The Southeastern Klamath Mountains And The Sierra Nevada, California, With Two Subspecies

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A NEW SPECIES OF *VACCINIUM* (ERICACEAE) FROM THE SOUTHEASTERN KLAMATH MOUNTAINS AND THE SIERRA NEVADA, CALIFORNIA, WITH TWO SUBSPECIES

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ABSTRACT

Vaccinium shastense J. K. Nelson & L. Lindstrand III (Ericaceae) is described as a new species from interior California. This new species is most similar to *V. parvifolium* Smith but differs by its ciliate, inrolled leaf margins, much wider hypanthium scar, dark blue, glaucous, quickly deciduous fruits, greater seed count, and pitted seed surface sculpturing. Moreover, *V. shastense* and *V. parvifolium* are allopatric, occur in distinct habitats, and have distinct genetic characters. Two subspecies of *Vaccinium shastense* are described: Vaccinium shastense subsp. shastense, endemic to the southeastern Klamath Mountains in Shasta County, California, and Vaccinium shastense subsp. nevadense J. K. Nelson & L. Lindstrand III from the western slope of the Sierra Nevada, California. The new subspecies differ from one another in flower color, length of persistent calyx ring, growth habit, geographic range and habitat, and distinct genetic characters. *Vaccinium shastense* subsp. *shastense* and *Vaccinium shastense* subsp. *nevadense* are compared to morphologically similar taxa in California by inclusion of an updated species key.

Key Words: California endemic, Ericaceae, Shasta huckleberry, Sierra huckleberry, Sierra Nevada, southeastern Klamath Mountains, Vaccinium shastense subsp. shastense, Vaccinium shastense subsp. nevadense, western Shasta County.

An unusual Vaccinium was found in 1991 by the first author at Golinsky Mine, on the west side of Shasta Lake in western Shasta County, California, growing on acid mine drainage seeping from bedrock crevices. This Vaccinium most closely fit the description of V. parvifolium Smith with the exception of its obviously different, dark blue, glaucous fruits, and an anomalous habitat with high summer temperatures and very low humidity. Similar plants were found in 2003 and 2004 at several other locations in the southeastern Klamath Mountains around Shasta Lake, Shasta County, California. The unusual fruit color, combined with the facts that these Shasta County populations are disjunct from the nearest putative V. parvifolium populations by at least 64 km and that they occur in a much more xeric region and habitat, led us to suspect them to be an undescribed taxon. While investigating the relationship between the Shasta County plants and V. parvifolium from coastal California and the Pacific Northwest, we learned of other V. parvifolium collections from the Sierra Nevada with dark fruits, even farther disjunct from coastal V. parvifolium. We expanded our research to include Sierra Nevada V. parvifolium populations, with the goal of determining the relationships among V. parvifolium and the putative new taxa in Shasta County and the Sierra Nevada. Our data show morphological, ecological, and genetic distinctions warranting description of two new *Vaccinium* taxa.

TAXONOMIC TREATMENT

Vaccinium shastense J. K. Nelson & L. Lindstrand III, sp. nov. (Fig. 1) "Shasta Huckleberry". ---TYPE: USA, California, Shasta Co., Golinsky Mine, 40°46′11″N, 122°26′32″W; T34N R5W S33 NE½, ca. 609 m (2,000 ft), 29 August 2012, *L. Lindstrand III s.n.* (holotype: CAS; isotypes: CHSC, DAV, GH, HSC, JEPS, MO, NY, OSC, RSA, STNF, US).

Shrub 0.5–1.7 m, crown-forming or rhizomatous; branches alternate, twigs green and strongly angled, glabrous. Plants erect to decumbent, growing as individual shrubs to rhizomatous thickets or ground covers. Bark of older branches brown to gray, striated. Leaves deciduous, alternate, thin, green and glabrous above, pale below with scattered short hairs, 1.2–4.6 cm long, 0.7–2.7 cm wide, ovate to obovate, base rounded to tapered, tip acute to obtuse, often with mucro; petiole 1 mm; margin entire to occasionally finely serrulate, ciliate with short, forward-pointing, gland-tipped bristles 0.2-0.6 mm long, margin often rolled under and therefore obscuring the ciliate margins. Flowers borne individually in lower axils of new shoots; pedicels recurved, ca. 1 cm long; flowers broadly urceolate, about as

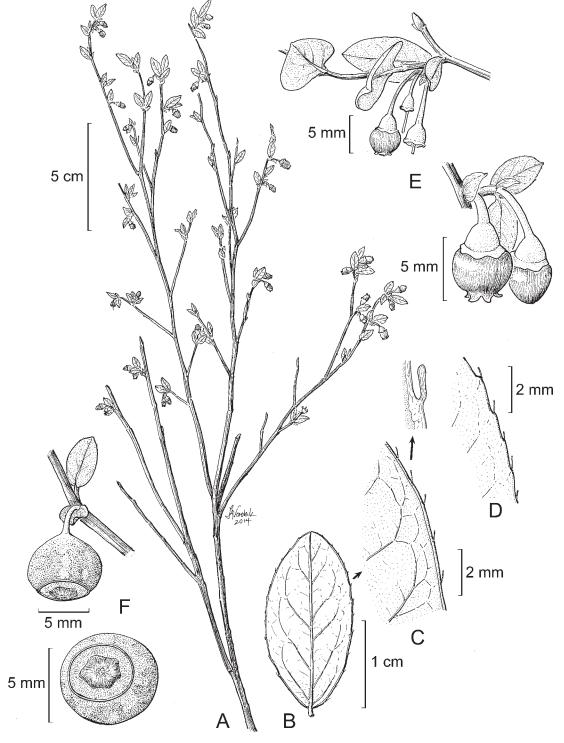


FIG. 1. Vaccinium shastense. A. Habit of plant in flower; B. Leaf, adaxial side; Leaf margin, C adaxial, D abaxial, showing forward-pointing marginal cilia; E. Flowers; F. Fruits showing wide hypanthium scar. Drawing by Linda A.Vorobik.

wide as long, with narrow mouth and five short spreading corolla lobes, anthers awned, with tubes longer than the awns. Flowers bright pink to greenish, occasionally whitish, flowering mainly December through June, with occasional flowering after summer rain events, calyx undulate, persisting in fruit as a ring 0.2–1.0 mm long on the distal end of the berry on dry specimens; fruit dark blue, glaucous, 6–8 mm in diameter, with wide persistent calyx ring and hypanthium scar > 3/4 the width of the mature berry; berries quickly deciduous with pedicels still attached. Seeds 1.1–1.2 mm long, 54–108 per fruit, surface pitted.

In addition to different phenotypic and ecological characteristics, *V. shastense* is also genetically distinct from *V. parvifolium*. Recent analysis of microsatellite loci identified high levels of genetic differentiation between *V. shastense* and *V. parvifolium* populations from the coastal regions of northern California, Oregon, and Washington (DeWoody et al. 2012).

Two disjunct *Vaccinium shastense* population groups occur; one in the southeastern Klamath Mountains, California, and one on the western slope of the Sierra Nevada, California. We describe these distinct groups as two subspecies.

Vaccinium shastense subsp. shastense

Shrub 0.5–1.7 m. Flowers bright pink to pale pink or greenish, occasionally whitish, flowering December through May. Calyx undulate, persisting in fruit as a ring 0.2–0.5 mm long on the distal end of the berry on dry specimens.

Paratypes: USA, CALIFORNIA. Shasta Co.: Little Backbone Creek, above confluence with Shasta Lake, 40°45′39″N, 122°26′10″W; T34N R5W S33, ca. 335 m (1100 ft), 13 May 2009, L. Lindstrand III s.n. (CAS, CHSC, JEPS); Friday-Louden Mine site, along County/USFS Road 5G012, in small tributary to Shoemaker Gulch, 40°45′12″N, 122°27′35″W; T33N R5W S5, ca. 731 m (2400 ft), 18 May 2009, L. Lindstrand III s.n. (CAS, HSC, JEPS); Squaw Creek, above confluence with Shasta Lake, 40°44′22″N, 122°28′10″W; T33N R5W S7, ca. 335 m (1100 ft), 27 May 2009, L. Lindstrand III & H. Kelly s.n. (CAS, JEPS, STNF); Bully Hill, along a small tributary stream to Horse Creek downstream of a former mine site at Bully Hill, Squaw Creek Arm of Shasta Lake, 40°47′73″N, 122°12′35″W; T34N R3W S21, ca. 335 m (1100 ft), 29 June 2009, L. Lindstrand III et al. s.n. (CAS, JEPS); Ingot, in unnamed stream tributary to Little Cow Creek, below Coronado Mine, 40°44′05″N, 122°04′11″W; T33N R2W S11 NW¹/₄, ca. 381 m (1250 ft), 30 April 2014, L. Lindstrand III s.n. (CAS, CHSC, DAV, HSC, JEPS, STNF).

Vaccinium shastense subsp. shastense most commonly occurs as individual shrubs up to 1.7 m in height (Fig. 2) and occasionally in dense



FIG. 2. Typical crown forming shrub habit of *Vaccinium shastense* subsp. *shastense*. Little Backbone Creek, Shasta County, CA. Photo by Len Lindstrand III.

rhizomatous colonies. Older stems tend to die and are replaced by new growth, giving the shrub an abundance of thatch in its interior. The old stems and new growth give the shrub a distinctive broomlike habit, particularly in winter when the stems are leafless. Flowering extends from December through May, with peak flowering in March and April, and opportunistic flowering based on local weather conditions has been observed through September. Plants may flower and fruit more than once during a single growing season; individual shrubs have been observed simultaneously bearing flowers, green fruits, ripe fruits, and overmature dried fruits. Flowers are usually bright pink at anthesis, occasionally paler pink (Fig. 3).

DISTRIBUTION AND HABITAT

Vaccinium shastense subsp. shastense occurs in the southeastern Klamath Mountains geomorphic



FIG. 3. Bright pink flowers of *Vaccinium shastense* subsp. *shastense*. South Fork Mountain, Shasta County, CA. Photo by Len Lindstrand III.

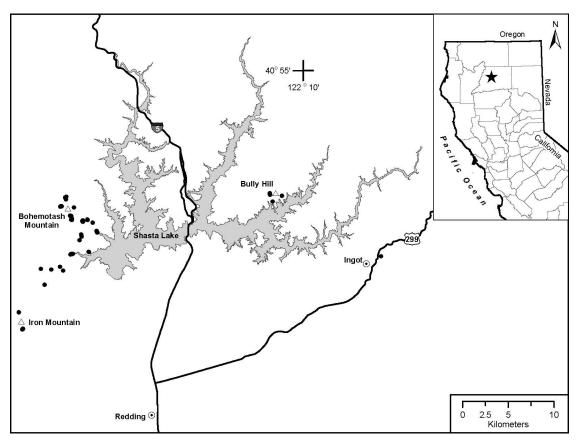


FIG. 4. Distribution of *Vaccinium shastense* subsp. *shastense* (dark circles), southeastern Klamath Mountains, Shasta County, CA.

province (Miles and Goudy 1997) in the vicinity of Shasta Lake, Shasta County, California. This area is characterized by mild, wet winters and hot, dry summers. The average annual precipitation is approximately 156 cm, occurring primarily as rainfall. Average annual temperatures range from 10°C in winter to 32°C in summer. The westernmost population is located at the headwaters of Slickrock Creek, approximately 1 km northwest of Iron Mountain. The easternmost population occurs near Ingot, in the Little Cow Creek watershed approximately 5 km southeast of Shasta Lake. The subspecies range includes three distinct localities: an approximately 46 km² area generally southwest of Shasta Lake from the vicinity of Iron Mountain northeast to the southern headwaters of Fall Creek, near Bohemotash Mountain; an approximately 1 km² area in the vicinity of Bully Hill on the Squaw Creek Arm of Shasta Lake; and a small area in an unnamed stream tributary to Little Cow Creek in the vicinity of Ingot (Fig. 4).

Vaccinium shastense subsp. shastense occurs at elevations between 326–1219 m. All known populations occur in western Shasta County and are located within a region historically known as the Copper Belt of Shasta County,

which is divided into two districts; the West and East Shasta Copper-Zinc Districts. The copper deposits are found in acidic lava flows and pyroclastic rocks known from the Devonian Balakala Rhyolite and Triassic Bully Hill Rhyolite geologic units (California Division of Mines and Geology 1974) that occur in this area. Most soils in these areas are acidic residual soils derived from weathering of the parent materials. Additionally, the exposure of sulphide minerals found in these deposits to oxygen and water creates a mild form of sulphuric acid, which circulates through rock and cliff formations, old mine workings, and the surrounding lands, creating acidic water conditions in several local streams and other wetlands. The V. shastense subsp. shastense populations nearly exclusively occur in areas characterized by these acidic soil and water conditions. At many locations the species grows immediately downstream of historic mine adits and overburden in acidic soil and water. The species also regularly occurs along streams characterized by acid mine discharge water chemistry. Other populations occur as understory shrubs in conifer forests, and in crevices and springs/seeps among rock outcrop or cliff features



FIG. 5. Typical rhizomatous patch habit of *Vaccinium shastense* subsp. *nevadense*. Alpha Road, near Alpha Diggings, Nevada County, CA. Photo by Len Lindstrand III.

characterized by seasonal or perennial acid water chemistry.

The V. shastense subsp. shastense populations are associated with riparian areas, springs/seeps, and other mesic environments in conifer forest, hardwood-conifer forest, and chaparral habitats. These forest and chaparral habitats are dominated by Arctostaphylos viscida Parry, Cornus nuttallii Audubon, Nolithocarpus densiflorus (Hook. & Arn.) Manos et al. var. echinoides (R. Br. ter) Manos et al., Pinus ponderosa Lawson & C. Lawson, *Pseudotsuga menziesii* (Mirb.) Franco var. menziesii, Quercus chrysolepis Liebm., Q. kelloggii Newb., Styrax redivivus (Torr.) L.C. Wheeler, and Toxicodendron diversilobum (Torr. & A. Gray) Greene. Species typically associated with V. shastense subsp. shastense include Acer macrophyllum Pursh, Aruncus dioicus (Walter) Fernald var. acuminatus (Rydb.) H. Hara, Calycanthus occidentalis Hook & Arn., Alnus



FIG. 6. Greenish to pale pink flowers of *Vaccinium shastense* subsp. *nevadense*. Bean Creek Road, Butte County, CA. Photo by Len Lindstrand III.

rhombifolia Nutt., Panicum acuminatum Sw. var. fasciculatum (Torr.) Lelong, Philadelphus lewisii Pursh, Polystichum californicum (D.C. Eaton) Diels, Pteridium aquilinum (L.) Kuhn var. pubescens Underw., Rhododendron occidentale (Torr. & A. Gray) A. Gray, R. columbianum (Piper) Harmaja, Rubus armeniacus Focke, R. ursinus Cham. & Schltdl., Salix lasiandra Benth. var. lasiandra, and Woodwardia fimbriata Sm.. Plant taxonomy follows Baldwin et al. (2012).

Vaccinium shastense subsp. nevadense J. K. Nelson & L. Lindstrand III, subsp. nov. "Sierra Huckleberry" --- Type: USA, California, Butte Co., Bean Creek Road, ca 0.8 km north of Little Bald Rock, in an unnamed drainage tributary to Brush Creek, 39°39'43"N, 121°19'29"W; T21N R6E S20 SE¼, ca. 1021 m (3350 ft), 5 June 2013, L. Lindstrand III s.n. (holotype: CAS; isotypes: CHSC, DAV, JEPS, STNF).

Shrub 0.5–1.5 m. Flowers pale pink to greenish, occasionally whitish, flowering March through June. Calyx undulate, persisting in fruit as a ring 0.4–1.0 mm long on the distal end of the berry on dry specimens.

Paratypes: USA, CALIFORNIA. El Dorado Co.: Ferrari Mill Road, in a forest drainage, ca. 1.6 km south of Jenkinson Lake, 38°41′58″N, 120°33′58″W; T10N R13E S20 SW ¼, ca. 1158 m (3800 ft), 1 July 2013, J. DeWoody et al. s.n. (CAS); Rock Creek Road, in a forest drainage at the intersection with USFS road 12N79, ca. 1.8 km west of Bald Mountain Lookout, 38°54′30″N, 120°43′34″W; T13N R12E S11 NW1/4, ca. 1036 m (3400 ft), 1 July 2013, J. DeWoody et al. s.n. (CAS). Mariposa Co.: Yosemite National Park, Big Creek, about 1 stream mile above the crossing of the Chowchill Mountain Road, westerly side of the stream, 37.50832/-119.66043, T5S R21E S10, ca 4630 ft, 10 July 2009, D.W. Taylor et al. 20671 (JEPS, YM); Yosemite National Park, tributary headwaters of Moss Creek, north of Big Oak Flat Road and south of Rockefeller Grove Road, on banks of small permanent stream, 250429/-4183389, ca. 1,820 meters (5970 ft), 14 August 2009, A. Colwell 09-399 (YM). Nevada Co.: Scotts Flat Reservoir, in forest drainage near the intersection of Scotts Flat and Casci Roads, and Scott Flat Campground, 39°17′03″N, 120°55′33″W; T17N R9E S1 NW 1/4, ca. 975 m (3200 ft), 28 June 2013, L. Lindstrand III & J. DeWoody s.n. (CAS, CHSC, DAV, JEPS); Alpha Road, on a sericite rock outcropping ca. 0.3 km north of Highway 20, 39°19′35″N, 120°47′09″W; T17N R10E S19 SW¹/₄, ca. 1371 m (4500 ft), 28 June 2013, L. Lindstrand III & J. DeWoody s.n. (CAS, JEPS). Plumas Co.: ca. 0.8 km north of Sly Creek Dam, in an unnamed drainage tributary to French Creek ca. 0.8 km northwest of the intersection

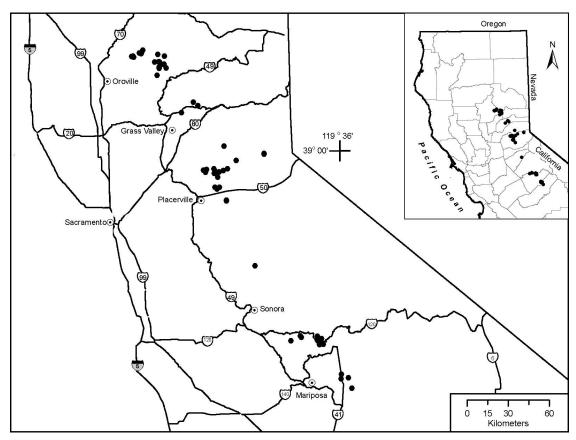


FIG. 7. Distribution of Vaccinium shastense subsp. nevadense (dark circles), west slope Sierra Nevada, CA.

of USFS roads 21N16 and 21N13, 39°37′15″N, 121°06′24″W; T20N R8E S5 NW ¼, ca. 1188 m (3900 ft), 5 June 2013, *L. Lindstrand III s.n.* (CAS, CHSC, DAV, HSC, JEPS, STNF). Tuolumne Co.: Greeley Hill, in vicinity of Red Cloud Mine, south end of Smith Ridge, on gravel USFS road 2.5 miles south of its junction with Moore Creek Road off of the Coulterville Road, in dry shallow gulch near ridgetop, 37.76833/120.06252, T2S R17E S14 NW1/4 of NE1/4, ca. 1000 m (3280 ft), 28 September 2009, *A. Colwell et al. 09-571* (YM).

Vaccinium shastense subsp. nevadense occurs on the western slope of the Sierra Nevada from southeastern Butte County to eastern Madera County, California. The species most commonly occurs in dense rhizomatous colonies (Fig. 5) and occasionally as individual shrubs up to 1.5 m in height. Individuals in most populations have an overall more decumbent habit when compared to those of V. shastense subsp. shastense. Flowering extends from March to June. Vaccinium shastense subsp. nevadense also differs from subsp. shastense in its greenish to pale pink flowers (Fig. 6) and a longer persistent calyx ring on the fruit (0.5–1.0 mm long on dry specimens).

Besides several slightly different phenotypic characteristics, distinct ecological characteristics and geographic range (see Distribution and Habitat below), Vaccinium shastense subsp. nevadense is also genetically distinct from Vaccinium shastense subsp. shastense. Analysis of microsatellite loci showed significant genetic differentiation between the Shasta County and southern Sierra Nevada populations (DeWoody et al. 2012). Subsequent analysis of the same microsatellite loci also showed significant genetic differentiation between the Shasta County and northern Sierra Nevada populations, and found no evidence of a genetic cline between the Shasta Lake and the Sierra Nevada populations (National Forest Genetic Laboratory 2014). The species is absent from the Southern Cascades ecological region, which separates the Shasta County and Sierra Nevada populations.

DISTRIBUTION AND HABITAT

Vaccinium shastense subsp. nevadense occurs along the western slope of the Sierra Nevada geomorphic province (Miles and Goudy 1997) from the vicinity of Bald Rock, Butte County,



FIG. 8. Red, translucent fruit of *Vaccinium parvifolium* and narrow hypanthium scar. Photo by T. Abe Lloyd, courtesy of Salal, the Cascadian Food Institute.

California, south to Fresno Grove Big Trees, Madera County, California (Fig. 7). The north-south extent of its range is approximately 360 km and includes ten Sierra Nevada counties. The species occurs on various sedimentary, igneous, and metamorphic substrates including Mesozoic granitic rocks, Paleozoic marine rocks, Tertiary volcanic flow andesite rocks, and undivided pre-Cenozoic metavolcanic rocks (Jennings et al. 1977). Known populations occur at elevations between approximately 609–2011 m. The species is found in locations characterized by 89 to 200 cm of annual precipitation, which occurs as rainfall and snow, and many populations occur in areas subject to persistent snow.

Vaccinium shastense subsp. nevadense occurs as an understory shrub in low- to mid-elevation mixed conifer forests, and is occasionally found in disturbed locations such as road cuts and former mine sites. Habitats at known populations include mesic and shady draws, springs/seeps, meadow edges, riparian areas, and rock outcroppings. Species composition in these mixed conifer forest habitats varies by location and includes Abies concolor (Gordon & Glend.) Hildebr., Arbutus menziesii Pursh, Arctostaphylos manzanita Parry subsp. manzanita, A. viscida, Calocedrus decurrens (Torr.) Florin, Ceanothus cuneatus Nutt. var. cuneatus, Chrysolepis sempervirens (Kellogg) Hjelmq., Cornus nuttallii, Corylus cornuta Marshall subsp. californica (A. DC.) E. Murray, Notholithocarpus densiflorus var. echinoides, N. densiflorus var. densiflorus, Pinus lambertiana Douglas, P. ponderosa, Pseudotsuga menziesii var. menziesii, Quercus chrysolepis, Q. kelloggii, and Taxus brevifolia Nutt. Species typically associated with V. shastense subsp. nevadense include Adenocaulon bicolor Hook., Alnus rhombifolia, Amelanchier alnifolia (Nutt.) M. Roem. var. semiintegrifolia (Hook.) C.L. Hitchc., Chimaphila umbellata (L.) W.P.C. Barton, Equisetum arvense L., Fragaria virginiana Mill., Frangula purshiana (DC.) J.G. Cooper subsp. annonifolia (Greene) Sawyer & S.W. Edwards, Goodyera oblongifolia Raf., Holodiscus



FIG. 9. Dark blue to purple, glaucous fruit of *Vaccinium shastense* and wide hypanthium scar. Golinsky Mine, Shasta County, CA. Photo by Len Lindstrand III.

discolor (Pursh) Maxim, Leucothoe davisiae A. Gray, Physocarpus capitatus (Pursh) Kuntze, Pteridium aquilinum var. pubescens, Rhododendron columbianum, R. occidentale, Rubus parviflorus Nutt., Sorbus scopulina Greene, and Symphoricarpos mollis Nutt.

IDENTIFICATION AND TAXONOMIC RELATIONSHIPS

Vaccinium shastense strongly resembles V. parvifolium superficially in its deciduous habit, green angled twigs, and number and placement of flowers. The most obvious difference between V. parvifolium and V. shastense is in fruit color and hypanthium scar dimensions; V. parvifolium has red translucent berries without surface waxy bloom (hence the common name red huckleberry) with a narrow hypanthium scar (Fig. 8), whereas



FIG. 10. Fallen *Vaccinium shastense* subsp. *shastense* fruit with pedicels attached. Golinsky Mine, Shasta County, CA. Photo by Julie Kierstead Nelson.

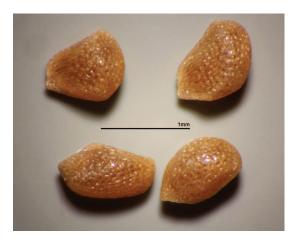


FIG. 11. Pitted seed surface of *Vaccinium shastense*. Photo by Martin Lenz.

V. shastense has dark blue to purple, glaucous fruits with a wide hypanthium scar (Fig. 9). Berries of both subspecies of V. shastense drop quickly after ripening, with pedicels still attached (Fig. 10), unlike those of Vaccinium parvifolium, which tend to persist on the shrub for at least two months (Vander Kloet 1988). Vaccinium shastense also has a pitted seed surface (Fig. 11) compared to the lengthwise striations found on V. parvifolium seeds (Fig. 12). Differentiating between the species in fruit is not challenging. Fortunately, there is also a consistent vegetative feature distinguishing the two species; namely, the leaf margin character. Vaccinium parvifolium leaves typically lack marginal cilia, whereas V. shastense leaves consistently have distinctive, forwardpointing multicellular marginal cilia (Figs. 1B, C, D; 13, 14). When present on V. parvifolium, the marginal cilia are confined to the lower third of the leaf margin and are 0.1–0.14 mm in length, whereas V. shastense leaves have marginal cilia

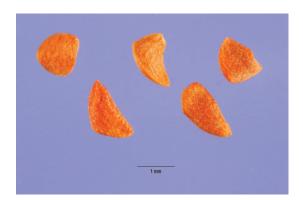


FIG. 12. Lengthwise striations on seed surface of *Vaccinium parvifolium*. Photo by Steve Hurst,, hosted by the USDA-NRCS PLANTS Database, http://plants.usda.gov/core/profile?symbol=VAPA.

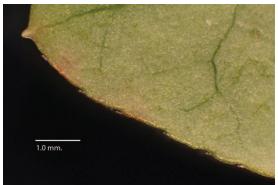


FIG. 13. Leaf margin of *Vaccinium shastense*. Photo by Martin Lenz.

that are 0.2–0.6 mm long (P. Fritsch, personal communication). *Vaccinium parvifolium* occasionally has strongly serrate leave margins, with teeth that may or may not be bristle-tipped. This strongly serrate leaf form has not been seen in either subspecies of *V. shastense*. Unlike *V. parvifolium*, which often grows on stumps and logs (Hitchcock and Cronquist 1973), *V. shastense* is confined to soil or occasionally rock crevices.

The third California species with strongly angled, green twigs is *V. scoparium* Leiberg ex Coville, a diminutive plant with serrate leaves (*V. shastense* leaves are entire), tiny flowers (<4 mm long, compared to 1 cm for *V. shastense*) and smaller red berries (3–6 mm diameter, compared to 6–8 mm blue berries for *V. shastense*). The anthers of *V. shastense* are awned (Fig. 15), as are those of *V. parvifolium* and *V. scoparium*.

Vaccinium parvifolium and V. shastense do not appear to be sympatric, as V. parvifolium is restricted to the coastally influenced regions of California and the more mesic parts of the western and high Klamath Mountains of Siskiyou County, extending northward, west of the Cascade Crest, through Oregon and Washington to British Columbia and Alaska. Vaccinium

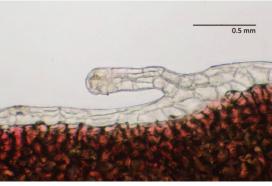


FIG. 14. Marginal cilium of *Vaccinium shastense* leaf. Photo by Martin Lenz.



FIG. 15. Awned anthers of *Vaccinium shastense*. Photo by Martin Lenz.

shastense is a species of inland California, from the southeastern Klamath Mountains and Sierra Nevada; these are areas with hot summers and absent coastal climate influences. Vaccinium shastense is endemic to California and plants with the overall habit of this and V. parvifolium can safely be determined by geographic location alone. The combination of vegetative and fruiting characteristics and distinct geographic ranges make identification of V. parvifolium, V. shastense subsp. shastense, and V. shastense subsp. nevadense straightforward.

In California, *V. scoparium* is restricted to the Klamath and Cascade Mountains of Del Norte, Humboldt, Siskiyou and Trinity Counties, where it grows in montane conifer forests. The species has been not been collected from Shasta County or the Sierra Nevada. *Vaccinium scoparium* and *V. shastense* are not sympatric.

Vaccinium shastense subsp. shastense differs from V. shastense subsp. nevadense in more subtle characters of growth habit, flower color, and length of persistent calyx ring on the fruit (see key below). The two subspecies of V. shastense are also genetically distinct, and disjunct, with the southern Cascade Range of California lying between the southeastern Klamath Mountains distribution of V. shastense subsp. shastense and the Sierra Nevada distribution of V. shastense subsp. nevadense (Fig. 16). Thus, the subspecies identification can also be determined by geographic location, absent other characters.

HISTORY OF *VACCINIUM* SHASTENSE COLLECTIONS

Vaccinium shastense subsp. shastense was first collected on April 30, 1900 near the Afterthought Mine (present day Ingot location, northeast of Redding) by Milo Baker, who wrote in his field book: "A small bush with the appearance of a huckleberry, yet from my recollections of the bush, this is different. This however is only an impression." (Book C, Milo S. Baker papers).

A second collection was made by James McMurphy on June 10, 1914 from "hill above mine, Kennet." Kennett was a town and the location of a copper smelter that processed ore from the many mines around what is now Shasta Lake; Kennett itself lies under the lake's waters now, not far from Shasta Dam. These collections represent the only two made before the first author discovered the plant growing at Golinsky Mine, on the west side of Shasta Lake, on June 7, 1991.

Vaccinium shastense subsp. nevadense is a different story, having been collected repeatedly up and down the Sierra Nevada for over a hundred and twenty years. J. W. Congdon collected the first specimens in 1893 from Mariposa County, and that same year by A. M. Carpenter from Nevada County. Specimens were collected over the years by many famous twentieth-century California botanists: John Thomas Howell, Enid Michael, Lewis S. Rose, G. Thomas Robbins, W. L. Jepson, and L. R. Heckard. Plants from the northern Sierra Nevada counties of Butte (1966), Plumas (1975), and Yuba (1994), were documented later than those of the central Sierra Nevada. Gehrung (2001) made note of these plants in her thesis on section *Myrtillus* in northern California, where she described plants from Plumas National Forest as anomalous V. parvifolium that were rhizomatous, with blue berries, and "pedicels that come off with the berries when picked" (pg. 60).

The "blue-berried red huckleberry" would have remained an unexplored curiosity but for a 2003 proposal by the U. S. Bureau of Reclamation to enlarge Shasta Lake by raising Shasta Dam, leading to intensive field surveys, discovery of additional *Vaccinium* populations west of Shasta Lake, and funds to investigate the genetic relationship of these plants to red-fruited typical *V. parvifolium*. Alison Colwell of Yosemite National Park made several collections of blueberried, decumbent plants from Tuolumne County, and brought them to our attention in 2009; at that point we broadened our study of anomalous blue berried *V. parvifolium* beyond Shasta County to encompass the Sierra Nevada plants.

RARITY AND CONSERVATION STATUS

Vaccinium shastense subsp. shastense is endemic to the southeastern Klamath Mountains in the general vicinity of Shasta Lake, Shasta County, California. The species is known from more than 20 occurrences at 14 general locations (Fig. 4), ranging from several isolated plants to 1000+plants occurring over large areas. Vaccinium shastense subsp. shastense appears to have specific ecological microhabitat requirements related to acidic edaphic and water conditions. Habitat is restricted to locations where natural geologic characteristics or historic mining disturbances provide these acidic conditions and

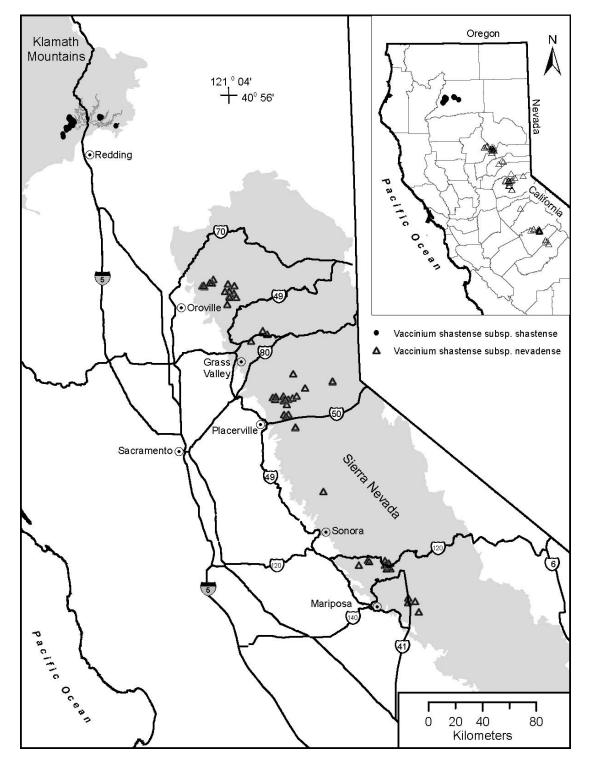


FIG. 16. Southeastern Klamath Mountain distribution of *Vaccinium shastense* subsp. *shastense* and Sierra Nevada distribution of *Vaccinium shastense* subsp. *nevadense*, California. Ecological unit boundaries from Miles and Goudy (1997).

adequate soil moisture. Specifically, *V. shastense* subsp. *shastense* populations are directly correlated to habitats with geologic characteristics causing naturally occurring acidic conditions, or former copper mine sites and adjacent areas affected by those activities where acidic conditions occur and have been exacerbated. *Vaccinium shastense* subsp. *shastense* does not occur in similar habitats not influenced by either naturally occurring acidic conditions or the mining activities that have produced these acidic conditions.

Many of the *V. shastense* subsp. shastense localities are disturbed habitats, including roadside ditches and road-cuts, overburden from mine adits, drainages and eroded slopes, riparian zones in streams characterized by acid mine discharge water chemistry, and forested slopes in areas formerly denuded of vegetation due to copper smelting during the early 1900s. Undisturbed localities include rock outcrop and cliff formations, and forested slopes and drainages. The species is adapted to survive fire, as basal sprouting and rhizomatous spreading have been observed by the second author in individuals and populations subjected to wildfire. Vaccinium shastense subsp. shastense could be useful for mine reclamation on moist, acidic sites within its narrow geographic range.

Vaccinium shastense subsp. shastense is rare in terms of its number of known populations and narrow geographic distribution; however, based on the distribution, size, and remoteness of most populations, their resilience to a variety of disturbances, and the type and level of known

or potential threats, the species is not presently endangered or threatened. The species is, however, narrowly endemic and uncommon such that its status should be monitored. We recommend that V. shastense subsp. shastense be considered for a California Rare Plant Rank of 1B.3 (Plants Rare or Endangered in California and elsewhere; not very threatened in California (<20% of occurrences threatened/low degree and immediacy of threat or no current threats known) in the California Department of Fish and Wildlife (CDFW) Special Vascular Plants, Bryophytes, and Lichens list (CDFW 2014) and the California Native Plant Society's (CNPS) Inventory of Rare and Endangered Vascular Plants of California (CNPS 2001, 2014).

Vaccinium shastense subsp. nevadense occurs along the western slope of the Sierra Nevada. The species north-south range extends approximately 360 km across ten counties. Although somewhat uncommon and irregularly distributed, the species is known from over 100 occurrences and appears fairly widespread across its range (Fig. 7). Most known occurrences are located in remote or fairly remote forest areas, including National Forest, California State Forest, and National Park lands. Given the number and locations of known populations, size of the species range, and the type and level of known or potential threats, recommendation of any regulatory status or conservation rank for Vaccinium shastense subsp. nevadense does not appear warranted.

Key to California Vaccinium, with V. shastense Taxa Included

Key to Vaccinium from Baldwin et al. (2012), modified to add V. shastense and subspecies.

- 1. Leaves evergreen, leathery, veins not prominent abaxially; pedicel jointed to flower; filaments ± hairy
- 1'. Leaves deciduous (rarely evergreen in young plants of V. parvifolium), thin or \pm thick, veins generally prominent abaxially; pedicel not jointed to flower; filaments glabrous

 - 3' Leaf serrate or minutely so, or ciliate (but see *V. parvifolium*); calyx lobes ± 0 or generally <tube, deciduous; twigs angled or not, green or not; flowers often 1 in axils of lowest leaves of youngest shoots
 - 4. Twigs strongly angled, green; fruit red to dark blue or purple
 - 5. Leaves ciliate with forward-pointing bristles 0.2–0.6 mm long, margins inrolled; otherwise entire or barely serrate; fruits dark blue, glaucous; hypanthium scar >3/4 width of berry
 - 6. Persistent calyx ring on berry 0.2–0.5 mm long on dry specimens, growth habit generally erect, occasionally rhizomatous, often crown forming shrubs 5–17 dm tall; flowers bright pink to pale pink; western Shasta County.... subsp. shastense

- 5' Leaves not ciliate or occasionally ciliate on lower third, cilia if present 0.1–0.14 mm long; fruits red, translucent, not glaucous; hypanthium scar up to 1/2 the width of berry.
- 4' Twigs not or weakly angled, ± green or yellow-green but not green; fruit not red (rarely dark red in *V. membranaceum* Douglas ex Torr.)

 - 8' Plant generally <5 dm; twigs not or weakly angled; leaf generally oblong or elliptic to obovate or oblanceolate, rarely elliptic, generally 1–3.5 cm, generally thin but not membranous, base tapered, tip seldom acute

ACKNOWLEDGMENTS

We thank the U.S. Bureau of Reclamation Mid-Pacific Region office for their support. We also thank Alison Colwell, for alerting us to the presence of "V. parvifolium" in the southern Sierra Nevada, her participation in the 2009 genetic study, for reviewing V. parvifolium specimens in several distant herbaria and discovery of characters that helped separate V. parvifolium from the Shasta County and Sierra Nevada plants, and for suggesting that seed coat morphology might be another distinction. Additional thanks go to Martin Lenz for counting and photographing the tiny seeds and other characters of V. shastense subsp. shastense, Matt Brown for leading us to sampling locations for genetic analysis in the El Dorado National Forest, Peter Fritsch for pointing out differences in cilia length between V. parvifolium and V. shastense, to Jennifer DeWoody and Valerie Hipkins for genetic analysis illuminating the patterns of difference among the Vaccinium in question, and to Barbara Wilson for reviewing a preliminary draft of the manuscript. We also thank Linda Vorobik for her marvelous illustration of V. shastense; T. Abe Lloyd for allowing use of his red huckleberry photo; and finally, we thank two anonymous reviewers of the draft manuscript for their very helpful comments.

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APPENDIX

ADDITIONAL SPECIMENS EXAMINED

Vaccinium shastense subsp. shastense

USA. CALIFORNIA. Shasta Co.: Cow Creek Canyon, 1 May 1900, M. S. Baker (UC); Hill above mine, Kennett, 10 June 1914, J. McMurphy, s.n. (DS); West side Shasta Lake (Golinsky Mine), Shasta-Trinity National Forests, Shasta Lake Ranger District, 7 June 1991, J. K. Nelson 91-63 (JEPS); North Fork Little Backbone Creek, 1/4 mile west of Golinsky Mine, growing on creek edge in full sun, T34N R5W S28, 1 May 1992, J. K. Nelson 92009 (RSA); Friday-Louden Mine adit along County Road 5G12 to Bohemotash Mountain from Shasta Dam, west side of Shasta Lake, ca 20 miles NW of Redding, T33N R5W S5, 13 April 2004, *J. K. Nelson 2004-012* (CAS); Bully Hill Mine, north side of Shasta Lake at confluence of Squaw Creek and Pit River arms, small population in depression below mine road east of Town Creek, T34N R3W S15, 8 September 2006, J. K. Nelson & L. Lindstrand III 2006-045 (CHSC, JEPS); Golinsky Mine, along dry slopes, wet seeps, and seasonal drainages on slopes below former Golinsky Mine site, Little Backbone Creek, Shasta Lake, T34N R5W S28, 11 May 2009, L. Lindstrand III s.n. (CAS, CHSC, JEPS); Little Backbone Creek watershed, Golinsky Mine, T34N R5W S28, 28 June 2011, J. K. Nelson et al. 2011-33 (CHSC); Friday Louden mine adit, adjacent to County Road 5GO12, west slope of Shasta Lake, ca 2 mi NW of Shasta Lake, 8 July 2011, J. K. Nelson & T. Derksen 2011-035 (CAS, CHSC, DAV, HSC, JEPS, STNF); Northwest of Bohemotash Mountain, along unnamed headwater stream tributary to Fall Creek, T34N R5W S19, 21 September 2011, L. Lindstrand III s.n. (CAS, CHSC, DAV, HSC, JEPS, STNF); Southwest slope of Bully Hill, along stream and below old copper mine workings, T34N R3W S16, 17 October 2012, L. Lindstrand III s.n. (CAS, CHSC, DAV, HSC, JEPS, STNF); West of Bohemotash Mountain, on forested slope above unnamed headwater stream tributary to North Fork Squaw Creek, T34N R5W S19 SW 1/4, ca. 1158 m (3800 ft), 10 October 2012, L. Lindstrand III & J. K. Nelson s.n. (CAS, CHSC, DAV, HSC, JEPS, STNF); Whiskeytown-Shasta Trinity National Recreation Area, along forest road 35N05 (Westside Road) at Friday Louden Mine adit, along a tributary stream of Shoemaker Gulch above Shasta Lake, T33N R5W S5, 18 June 2012, P. Fritsch et al. s.n. (CAS); Northwest of Bohemotash Mountain, along unnamed headwater stream tributary to Fall Creek, T34N R5W S19, 26 April 2013, L. Lindstrand III s.n. (CAS, CHSC, DAV, JEPS, STNF); Ingot, in unnamed stream tributary to Little Cow Creek, below Coronado Mine, T33N R2W S11 NW 1/4, 5 September 2014, L. Lindstrand III & J. K. Nelson s.n. (CAS, CHSC, DAV, HSC, JEPS, STNF); Northwest slope of Iron Mountain, in draw at the headwaters of Slickrock Creek, T 33N R 6W S28SE 1/4, 26 September 2014, L. Lindstrand III s.n. (CAS, CHSC, DAV, HSC, JEPS, STNF).

Vaccinium shastense subsp. nevadense

USA. CALIFORNIA. Butte Co.: Crossing of Lewis Creek with Lewis Creek Ridge Road, NW of Sly Creek Reservoir, 29 June 1966, C. R. Quick 66-34 (CAS); NE of Oroville at Little Bald Rock, T21N R6E S20, 14 June 1980, R. A. Schlising 3708 (CHSC); Swamp, where the road forks and crosses French Creek Reservoir, 15

September 1981, L. Ahart 3170 (CHSC, CAS); Along Bean Creek Road ca 4/5 mile east of Little Bald Rock, T21N R6E S29, 24 May 1983, J. D. Jokerst et al. 1778 (CHSC); Along dirt road 2 miles south of Milsap Bar, about 23 miles northeast of Oroville, 29 July 1983, L. Ahart 4221 (CHSC, CAS); Plumas National Forest, near Little Bald Rock, T21N R6E S20, 26 May 1987, L. Hanson 299 (CHSC); Ca 0.4 mi NW of Little Bald Rock, 0.2 mi E of Bald Rock Rd., T21N R6E S20, 26 April 1990, B. Castro 427 (CHSC); Northern high Sierra Nevada, narrow northeast-trending ridge overlooking South Branch Middle Fork Feather River, about 1.7 mi east of Milsap Bar, T21N R7E S7, 27 July 1994, L. P. Janeway 4701 (CHSC); Watson Ridge, about 3 mi northeast of Bald Rock Dome, T21N R6E S13, 8 May 1995, L. P. Janeway 4762 (CHSC, CAS); Watson Ridge on both sides of USFS Rd. 21N25A, T21N R6E S13, 16 October 1996, L. Gehrung 123 (CHSC); Northern high Sierra Nevada, along Bean Creek Road 1.1 km east of Bald Rock Road, T21N R6E S20, 25 May 2010, L. P. Janeway 92980 (CHSC); 0.5 air miles northeast of Little Bald Rock, northeast of and below Bean Creek Road, 0.6 miles from Bald Rock Road, 5 August 2011, P. Zika et al. 25710 (CAS); Bean Creek Road, ca 0.5 mi. north of Little Bald Rock, in an unnamed drainage tributary to Brush Creek, 2 April 2013, L. Lindstrand III s.n. (CAS, JEPS). Calaveras Co.: San Antonio Creek, 6 August 1906, W. R. Dudley s.n. (CAS); Trail to San Antonio Falls Calaveras, 17 June 1912, H. A. Walker 2738 (UC); 2 ½ miles east northeast of Creighton, Big Trees (Calaveras), 25 October 1935, W.R. Howden s.n. (UC). El Dorado Co.: Rock Creek El Dorado National Forest, T12N R11E S15, 13 May 1915, O. M. Evans (JEPS); Rubicon Springs, Tahoe region, 8 July 1922, H. M. Mitchell s.n. (CAS); 1 mi. west of Blair Saw Mill, El Dorado National Forest, 6 July 1934, P.L. Johannsen 369 (UC); 0.25 mi south of Bob's Cabin, El Dorado National Forest, Pyramid Peak Quad., T13N R13E S24, 9 October 1934, P. L. Johannsen 510 (UC); Along borders of Long Creek, 1-2 mi. from its confluence with South Fork American River, 28 May 1944, G. T. Robbins 1639 (CAS, UC); Along north shore of Rockbound Lake, Rockbound Valley, Desolation Valley Wilderness Area, T11N R12E S20-21, 5 August 1945, G. T. Robbins 2083 (CAS, UC); Watershed of Little Silver Creek, a tributary of Rock Creek on the south side of Georgetown Divide about 1/ 2 mile below summit, T13N R11E S9, 25 April 1960, R. E. Rockey 1 (CAS, JEPS, UC); About 7 mi east of Georgetown (along Pilot Creek, nw of Blodgett Forest headquarters), Pilot Creek, 30 May 1969, L. R. Heckard 2244 (JEPS); Blodgett Experimental Forest, 27 May 1970, J. T. Howell & G.H. True 46529 (CAS); Blodgett Forest, 27 May 1970, L. Rose 70044 (CAS); Blodgett Forest, 19 July 1973, J. T. Howell & P. Rubtzoff s.n. (CAS); Blodgett Forest: Chinquapin Flat Road ca. 1.6 mi. south of Gaddis Creek Road; ca. 175 yards down the southwest slope from road (Comp. 600R), forest floor ca. 75 yards up the slope from South Blodgett Road, 19 May 1976, P. Rubtzoff 8539 (CAS); Blodgett Forest: headquarters area (Comp. 250R), forest floor between Staff House and Bunkhouse, 19 May 1976, P. Rubtzoff 8543 (CAS); Slab Creek; ca. 1 air mile S of Pino Grande (site), eastern vicinity Blodgett Forest, T21N R12E S28, 21 June 2006, D. W. Taylor 19551 (JEPS). Madera Co.: Trail from Fresno Big Trees 13 July 1901, W. R. Dudley s.n. (CAS) (labeled as Fresno Co.); Fresno Grove Big Trees,

6 August 1931, W. L. Jepson 15972 (UC). Mariposa Co.: Red Cloud, 31 May 1893, J. W. Congdon s.n. (CAS, DS); Red Cloud, 1 June 1895, J. W. Congdon s.n. (UC); Near Wawona, 26 May 1924, J. T. Howell 353 (CAS); Merced Grove of Big Trees, 4 May 1934, E. Michael s.n. (CAS); Bean Creek, along Dogtown Road, at southernmost creek ford, 20 March 1977, D. W. Taylor 15924 (JEPS); Merced Grove where the road crosses Moss Creek just inside the park boundary, 28 June 2004, A. Colwell & C. Coulter AC 4-106 (UC); Yosemite National Park; old logging road south of Crane Flat campground, 30 June 2005, A. Colwell et al. AC 5-39 (UC); Yosemite National Park.; Unnamed drainage west of Crane Flat Campground about one mile from park boundary, 19 June 2007, D. Grossenbacher & L. Dennis 510 (UC); Tributary of Moss Creek south of Big Oak Flat Road, one km south southeast of Crane Flat Lookout, 26 June 2007, A. Colwell et al. Jul-78 (UC); Tributary headwaters of Moss Creek between Big Oak Flat Road and Rockefeller Grove Road, VAPA10-6 and LEDA10-6 plots, v 2.6 meters, 7 August 2007, A. Colwell 07-297 (UC). Nevada Co.: Along road at Scotts Flat L., 1 June (year unknown), L. S. Mott LM6717 (CAS); Nevada County, September 1893, A. M. Carpenter s.n. (UC); Nevada County, September 1893, A. M. Carpenter s.n. (UC); Alpha Road just north of Highway 20, 13 miles east of Nevada City, 23 August 1965, G. H. True & J. T. Howell 2446 (CAS); Scotts Flat Reservoir on Deer Creek about 5 miles east of Nevada City, 25 August 1965, G. H. True & J. T. Howell 2538 (CAS); Skillman Flat on Washington Ridge, ca. 12 mi. E. of Nevada City, 28 May 1970, J. T. Howell & G. H. True 5357 (CAS); South Fork of Yuba River ca. 1 mi. below Washington, 24 May 1971, G. H. True & J. T. Howell 6591 (CAS); Booth Point, 1 mi. north thereof, southerly rim Middle Yuba River Canyon, 29 July 2005, D.W. Taylor & T. Engstrom 19442 (JEPS); South Fork of Yuba River below Washington, 27 June 2013, L. Lindstrand III s.n. (CAS, JEPS). Placer Co.: Sugar Pine Tahoe National Forest, 16 May 1931, L. S. Smith 2452 (UC). Plumas Co.: Along Lost Creek, about 6 miles north of the Sly Creek Dam, 2 July 1975, L. Ahart 837 (CHSC, CAS); on French Creek, tributary to Sly Creek Reservoir, S side of USFS Rd. 21N16, T20N R8E S5, 1 September 1997, L. Gehrung 158 (UC); on French Creek, tributary to Sly Creek Reservoir, N side of USFS Rd. 21N16, T20N R8E S5, 1 September 1997, L. Gehrung 157 (UC). Tuolumne Co.: North Crane Creek Yosemite National Park, Yosemite Quad., T2S R20E S7, 21 June 1935, W. B. Augustine 155 (UC); 1 mi. NW Park Lookout; Stanislaus National Forest, Yosemite Quad., T2S R19E S13, 16 August 1935, C. M. Belshaw 64A (UC); Stanislaus River bridge near Twain Harte - Sierra Nevada, T2S R18E S4NE 1/4, 4 June 1954, J. T. Howell 29924 (CAS); South Fork Stanislaus River - Sierra Nevada, 5 June 1955, J. T Howell 30278 (CAS); In drainage cresting Pilot Ridge Sierra Nevada, Pilot Ridge, 8 July 1982, D. W. Taylor 8021 (JEPS); Above FS road 1S13, lower slopes of Pilot Ridge, South Fork Tuolumne River drainage, Stanislaus National Forest -Sierra Nevada, 27 April 1996, J. R. Shevock 13280 (CAS); North Crane Creek, 26 May 2004, A. Colwell & A. Sanders AC 4-10 (UC); North Crane Creek, 30 August 2004, A. Colwell & A. Sanders AC 4-129 (UC); Yosemite National Park, Rockefeller Grove Road, 400 m N of Big Oak Flat Road, 13 July 2005, A. Colwell et al. AC 5-71 (UC); Yuba Co.: On the south side of Schwartz Meadow, on the east side of La Porte Road, about 4 miles northeast of Strawberry Valley, T20N R8E S10, 27 June 1994, L. Ahart 7399 (CHSC, JEPS); ca 2 air miles E of Clipper Mills and ca 1.6 mi. NE of Big Hill, along USFS RD 20N04, on ridge between Hampshire and Missouri Creeks, T19N R8E S6, 23 April 1997, B. Castro 724 (CHSC). Unknown Co.: Tahoe Forest, 1 June 1913, G. M. Noyes 198 (CAS).