Egger, J.M. and R.E. O'Dell. 2026. *Castilleja benitoensis* (Orobanchaceae), a new serpentinite endemic from San Benito Mountain, California. Phytoneuron 2026-12: 1–75. Published 27 May 2026. ISSN 2153 733X

CASTILLEJA BENITOENSIS (OROBANCHACEAE), A NEW SERPENTINITE ENDEMIC FROM SAN BENITO MOUNTAIN, CALIFORNIA

J. MARK EGGER
Herbarium, Burke Museum of Natural History and Culture
University of Washington
Seattle, Washington
m.egger@comcast.net

RYAN E. O'DELL
Bureau of Land Management
Central Coast Field Office
Marina, California
rodell@blm.gov

ABSTRACT

Castilleja benitoensis Egger & O'Dell, **sp. nov.** is described, a narrow endemic of alluvial soils derived from serpentinite in riparian communities along perennial streams in the vicinity of San Benito Mountain, San Benito County, California. Its position in relationship to the taxa informally defined as the *Castilleja miniata* complex within the state of California is discussed, and a key to these taxa along with representative field photographs are provided to aid in their identification. The new species is sister to *Castilleja oblongifolia* A. Gray, recognized here at species rank as originally described.

Through a chance interaction while annotating recently posted observations of *Castilleja* species by others on the iNaturalist website in 2023, the authors began a discussion of an unusual member of that genus found in the vicinity of San Benito Mountain in the Inner South Coastal Ranges subregion of California. Though first collected by W.H. Brewer in 1861, this form was apparently not collected again until 1944 and was known from only a small number of herbarium collections until recently. The plants were annotated by various botanists as *Castilleja* sp., *C. affinis* Hook. & Arn., *C.* cf. *angustifolia* (Nutt.) G. Don, *C.* cf. *miniata* Douglas ex Hook., *C. montana* Congdon, *C. oblongifolia* A. Gray, *C. stenantha* A. Gray, and *C. subinclusa* Greene subsp. *subinclusa*. Most herbarium specimens were eventually annotated to *C. miniata* without infraspecific rank. A similar range of names was applied by users of iNaturalist to field photos of the plants in question, including by Egger, who at first glance, annotated a post of it as *C. subinclusa*. However, O'Dell, a botanist with broad knowledge of the San Benito Mountain flora, disagreed, pointing out the unique morphology and ecology of the San Benito plants, their closer resemblance to *C. miniata*, and their substantial disjunction from other populations of *C. miniata* in California.

After a more careful examination of specimens collected by O'Dell in late 2023 and an increasing number of observations and photos posted on Calflora and iNaturalist, the authors met on 8 September 2025 to examine, photograph, and collect voucher specimens from several populations of the unique *Castilleja* along Clear Creek and Sawmill Creek in the vicinity of San Benito Mountain. Following consideration of its unique combination of characters, specialized habitat and ecology, and highly limited and disjunct distribution, we propose its recognition at the rank of species.

CASTILLEJA BENITOENSIS J.M. Egger & R.E. O'Dell, **sp. nov. TYPE**: **California**. San Benito Co.: BLM Clear Creek Management Area, Sawmill Creek, 36.342839° N, 120.658251° W, banks of Sawmill Creek (perennial creek) in alluvium derived from serpentinite (New Idria serpentinite mass), with *Salix breweri*, *Solidago guiredonis*, *Aquilegia eximia*, *Pyrrocoma benitoana*, *Trichostemma rubisepalum*, *Parnassia palustris*, *Agrostis exarata*, *Helenium puberulum*, *Sisrynchium bellum*, 1164 m, 8 Sep 2025, *Mark Egger 1770* with Ryan O'Dell, (holotype: WTU, single plant mounted on two sheets, WTU-V-467468 and WTU-V-467467; isotypes: CAS, JEPS, US, WTU). Figures 1–9.

Differs from *Castilleja miniata* Douglas ex Hook. in its combination of (a) compact, relatively few-flowered inflorescences, (b) entire, often reduced, acuminate-tipped bracts that are only weakly differentiated from the distal leaves and are either lacking in distally contrasting coloration or are inconspicuous due to their reduced size, with a pronounced shift of bright inflorescence coloration to the conspicuous calyces and corollas, (c) unusually long, linear-acuminate, often spreading calyx lobes, (d) longer, densely ranked, often imbricate leaves of the proximal stems contrasting with the reduced, usually sparce, and often scale-like leaves on the distal stems, (e) dense but inconspicuous, strigillose-puberulent pubescence on stems and leaves below the inflorescence, (f) strict adaptation to alluvial soils derived from New Idria serpentinite in riparian communities along perennial streams, and (f) its widely disjunct and highly restricted distribution.

Plants herbaceous perennials from slender, woody, usually rhizomatous caudices, with a complex system of numerous radicant-tufted, fine to coarse, short to long, often branched and intertwined rootlets. **Stems** 1 to many (25+) and often including sterile caulicles, the above ground portion usually 0.5–1.3 m tall, erect-ascending, often becoming lax, widely spreading, and supported by nearby plants or nearly decumbent; unbranched to more often conspicuously branched from the distal half, the few to many branches 0.3–35 dm in length, arising alternately from the distal portion of the leaf bases and elongating in an ascending-erect manner to a terminal, spicate inflorescence, these together often corymbiform in appearance; dull, pale green to often pale to deep reddish-brown, especially in exposed sites; pubescence densely strigillose-puberulent with minute, white to translucent, eglandular trichomes below the inflorescence, rapidly becoming finely short-pilose in the inflorescence with erect, translucent trichomes mixed with short, stipitate-glandular ones. **Leaves** 1–3 veined, highly variable in size, and distribution, the proximals 30–70 mm x 2–6 mm and often ± imbricate with generally shorter internodes, the distals 3–30 mm x 1–4 mm and usually remote, with longer internodes and often appearing scale-like; sometimes with poorly developed axillary fascicles; entire, narrowly linear-lanceolate, smooth-margined, weakly to moderately involute, ascending-appressed with the distals often proximally sub-clasping, sessile and decurrent into ridges along the stem and often with an acute-tipped, triangular flange on each side of the base, 1–2 mm in length; distally acute to acuminate and often minutely cuspidate; dull, pale green to often pale to deep reddish-brown; both surfaces densely strigillose-puberulent as in stems. **Inflorescences** short compact and almost head-like to moderately spicate, 2–8(–12) cm long, relatively few-flowered, 2–8(–12) flowers per spike; flowers sessile, sometimes short-pedicellate in fruit, 1–3 mm long; bright coloration occurring primarily on the calyces and corolla beaks, sometimes on the distal portion of the bracts. **Bracts** 5–22 mm long, reduced and weakly differentiated from the distal leaves, usually appressed to and proximally sheathing the calyces, entire, proximals sometimes scale-like, sessile and decurrent as in leaves, narrowly lanceolate, often truncate proximally, acuminate distally; pubescence densely strigillous-pilosulous on both surfaces; proximals usually dull, pale green throughout or becoming red to orange-red distally, distals dull, pale green proximally becoming red to orange-red distally. **Calyces** 25–40 mm long, abaxial and adaxial clefts subequal, 15–25 mm long, usually ≥ 50% of the calyx length, lateral clefts 12–16 mm, usually ≥ 33% of the calyx length, the lobes formed thereby linear-acuminate; pubescence finely and densely pilose to pilosulous or lanulose, mixed with shorter, stipitate glandular trichomes; usually entirely red to orange-red except for pale green in the proximal portion of the tube. **Corollas** 40–53 mm long, the beak and tube about equal in length; the beak usually red to orange-red throughout

(sometimes yellow-orange proximally) and usually divided at the tip into two triangular, acute lobes, 1.0–1.5 mm in length, adaxial surface densely puberulent with both stipitate-glandular and eglandular trichomes, margins sparsely puberulent to glabrescent; tube usually stramineous, glabrescent to sparsely pilose; lower lip thickened and strongly reduced, 2.0–2.5 mm long, and divided into 3 subequal teeth about 1.0 mm long, incurved and the outer two sometimes splayed, acute-acuminate, glabrous, dark green or red throughout; stigma narrowly capitate and barely expanded, pale green or red, it and the distal portion of the style exserted from the beak; anthers four, about 1.0–1.5 x 0.1 mm, longitudinally dehiscent, stramineous, they and the distal filaments often pendulously exserted from the beak after pollination, pollen grains ca. 0.01 mm in diameter, stramineous. **Capsules** 13–15 mm x 6–7 mm, ovoid, with apiculate apex, smooth to obscurely alveolate, glabrescent; seeds numerous, ca. 80–100 per capsule. **Seeds** 1–2.5 mm, ovate to triangular or wedge-shaped, coats translucent, stramineous, loose-fitting, reticulate with smooth, very shallow tangential walls and inner walls membranous, persistent, smooth to rarely obscurely striate. **Chromosome number** unknown.

Flowering June-November; 760–1341 meters.

Additional collections examined. California. San Benito Co.: Diablo Range: San Carlos Creek drainage. San Carlos [= San Benito], near summit [ca. 36.399025, -120.675279], 20 Jul 1861, *Brewer 772* (GH, UC, US); San Benito Mountain Natural Area, ca. 4200 ft [ca. 36.386149, -120.664827], 6 Jul 1972, *Griffin 3234A* (JEPS); New Idria, reservoir [ca. 36.399383, -120.674492], 17 Jul 1986, *Yadon H-2783* (PGM); sandy soils close to a small serpentine creek near Aurora Grade, 950 m, [ca. 36.396201, -120.674955], 2 Aug 1998, *Sanchez-Mata s.n.* (DAV); Sawmill Creek drainage. 1 mi SE of San Benito Peak, 4400 ft [ca. 36.359380, -120.63910], 11 Aug 1944, *Storer 206* (UC); E of San Benito Mountain toward Santa Rita Peak, alluvium [ca. 36.359611, -120.628854], 13 Aug 1992, *Yadon H-4520* (PGM); BLM Clear Creek Management Area, Sawmill Creek, perennial riparian zone, 36.348155, -120.653170, 26 Oct 2023, *O'Dell s.n.* (GH, MO, NY, OSC, RENO, RM, WTU); Clear Creek drainage, in Clear Creek above New Idria, 4000 ft [ca. 36.38339961, -120.719799], 4 Jul 1934, *Lyon 309* (UC); serpentine slopes along Clear Creek, 18.8 mi from jct N of Bitterwater on road to New Idria, [ca. 36.360502, -120.761272, 1 Sep 1955, *Raven 8824* (CAS, JEPS); in stream and on banks of Clear Creek, ca. 3.3 mi SW of Idria, ca. 3200 ft. [ca. 36.383039, -120.717530], 14 Jul 1956, *Thomas et al. 13044* (CAS-DS); side canyon of Clear Creek Canyon, on Clear Creek Road, 5 mi E of jct with road to Coalinga, ca. 3200 ft [ca. 36.383884, -120.718756], 20 Oct 1958, *Chisaki et al. 1172* (JEPS); Clear Creek road, 7.05 mi E of Hernandez Valley road, ca. 3300 ft. [ca. 36.376291, -120.688224], 4 Jun 1960, *Hesse 2807* (UC); Clear Creek Road, 3.1 mi E of Coalinga road, ca. 2550 ft. [ca. 36.370542, -120.743456], 20 Jul 1965, *Hesse 3306* (JEPS); bank of the upper waters of Clear Creek, ca. 3000 ft., 36.3796, -120.7074, 9 Jun 1966, Myrick 1408 (SBBG); in heavily serpentinized moist soil, [ca. 36.369511, -120.748686], 2700 ft, *Twisselmann 12,847* (CAS); serpentine alluvium, perennial creek, 36.383818, -120.719482, 9 Aug 2017, *O'Dell s.n.* (SBBG); banks of Clear Creek, adjacent to Clear Creek Road, ca. 3270 ft., 36.378420, -120.704281, 8 Sep 2025, *Egger 1769 & O'Dell* (RSA, WTU). Note: all specimens with geolocations in parentheses were estimated by O'Dell.

Additional observations and photos. Numerous field observations of the species were made by O'Dell and uploaded to Calflora.org (Calflora 2026). These are currently identified as *Castilleja miniata* or *C. miniata* subsp. *miniata*. A few field observations by other observers have also been uploaded to Calflora and are similarly identified. Additional observations of the new species by several observers have been uploaded to iNaturalist.org (iNaturalist 2026). These observations have been examined by the authors and confirmed to be the *C. benitoensis.* These are currently listed as *C. miniata* on the website. The locations shown on Maps 1 and 2 are composites of herbarium specimens and verified images posted on Calflora. The iNaturalist posts all fall within the mapped occurrences.

Figure 1. Holotype of *Castilleja benitoensis*, on two sheets, *Egger 1700* with O'Dell, sheet B, distal half of single plant, WTU.

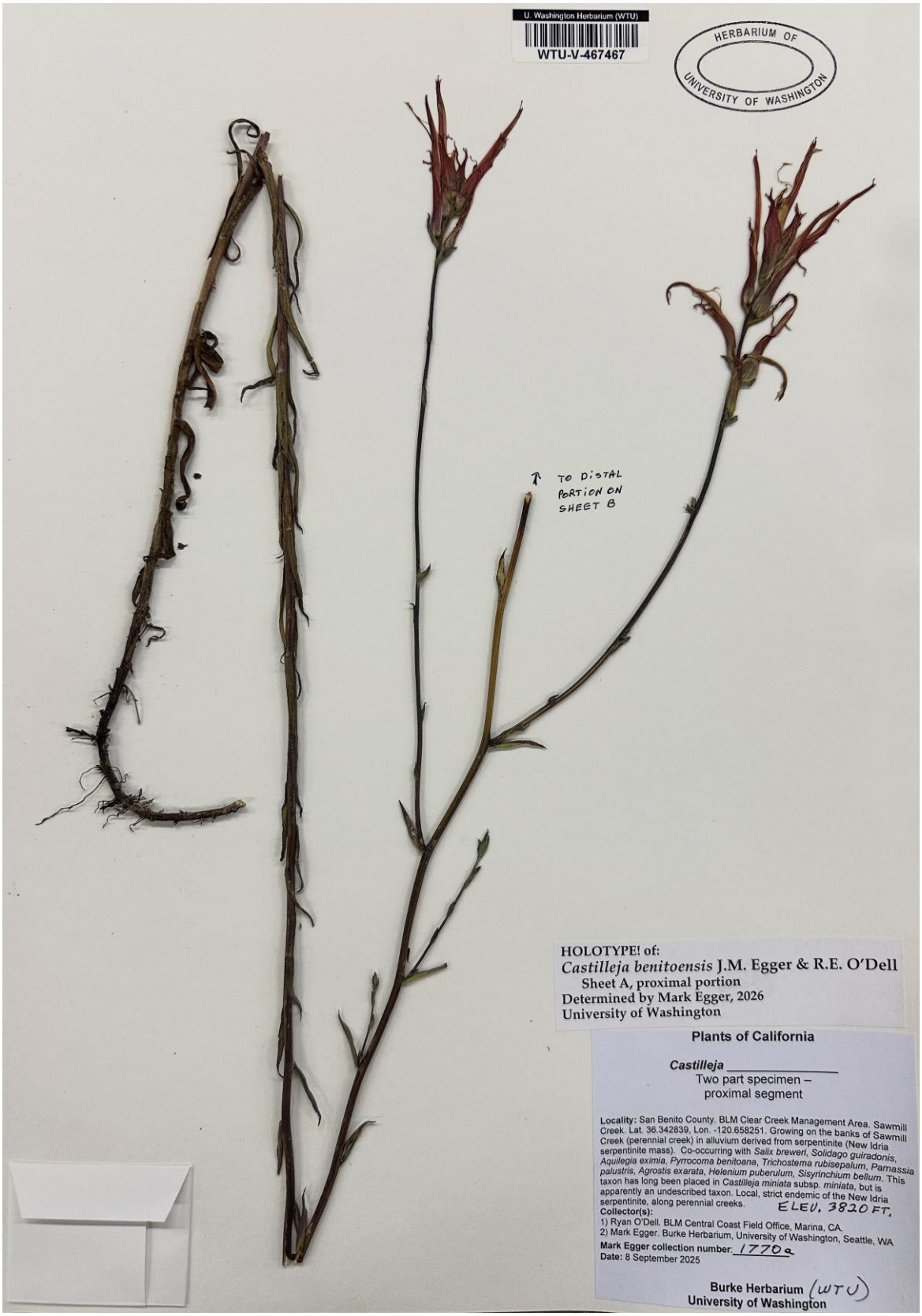


Figure 2. Holotype of *Castilleja benitoensis*, on two sheets, *Egger 1700* with O'Dell, sheet A, proximal half of single plant, WTU.

Figure 3. Closeup of bracts, calyces, corollas, and inflorescences, holotype plant of *Castilleja benitoensis*, *Egger 1700* with O'Dell, sheet B, distal half of single plant, WTU.

Figure 4. Holotype plant of *Castilleja benitoensis*, *Egger 1700* with O'Dell, distal portion of the plant before pressing at the type locality, 8 September 2025.

Figure 5. Holotype plant of *Castilleja benitoensis*, *Egger 1700* with O'Dell, single inflorescence from the plant before pressing at the type locality, 8 September 2025.

Figure 5. Holotype plant of *Castilleja benitoensis*, *Egger 1700* with O'Dell, closer view of single inflorescence from the plant before pressing at the type locality, 8 September 2025.

Figure 7. Holotype plant of *Castilleja benitoensis*, *Egger 1700* with O'Dell, a single-flowered inflorescence and distal-most leaf from the plant before pressing at the type locality, 8 September 2025. Note the notch at the apex of the corolla beak, forming two short lobes. This is unusual in most *Castilleja* species but occurs regularly in *C. benitoensis*.

Figure 8. Holotype plant of *Castilleja benitoensis*, *Egger 1700* with O'Dell, single inflorescence from the plant before pressing at the type locality, 8 September 2025.

Figure 9. Holotype plant of *Castilleja benitoensis*, *Egger 1700* with O'Dell, mid-stem and leaf detail, showing the typical minute, strigillose pubescence of the plant before pressing at the type locality, 8 September 2025. While difficult to see even up close, this pubescence covers almost every surface of the leaves and stems below the inflorescence, before transitioning rapidly into the more complex pubescence of the inflorescences.

Etymology. The new species is named for San Benito Mountain, in the vicinity of which its entire known distribution is contained. We suggest the English common name to be "San Benito Paintbrush."

Distribution, habitat, and associated species. *Castilleja benitoensis* is an obligate wetland species restricted to riparian zones (perennial creeks and seeps) of the New Idria serpentinite mass and serpentinite alluvial deposits downstream of it (Maps 1–2). Frequently associated species of this zone include *Salix breweri, Aquilegia eximia, Parnassia palustris, Stachys pycnantha, Trichostemma rubisepalum, Achillea millefolium, Helenium puberulum, Pyrrocoma benitoana, Solidago guiredonis, Sisrynchium bellum, Agrostis exarata, Elymus trachycaulus*, and *Muhlenbergia asperifolia*. The New Idria serpentinite straddles the San Benito County and Fresno County border in the Diablo Range (Inner South Coast Ranges) of central California. Thus far, *C. benitoensis* has been located only in San Benito County, though it likely also occurs in the adjacent portion of far southwestern Fresno County. The New Idria serpentinite mass is approximately 6 km wide by 20 km long with a total area of approximately 12,000 ha. The elevation ranges from 760 m at Hernandez Valley (San Benito River) to a maximum of 1,600 m on San Benito Mountain. At the lowest elevation, minimum average temperature is 7°C in winter, and maximum average temperature is 22°C in summer (Remote Automated Weather Stations 2026). Average annual precipitation is 40 cm, mostly as rain in winter. The Köppen-Geiger climate is Csa hot summer mediterranean (Beck et al. 2023). At the highest elevation, minimum average temperature is 5°C in winter, and maximum average temperature is 29°C in summer. Average annual precipitation is 51 cm, mostly as rain in winter, with occasional snow. The Köppen-Geiger climate is Csb warm summer mediterranean.

The New Idria serpentinite is unusual compared to all other ultramafic masses in California in that the rock is highly sheared and crushed (Coleman 1996; Coleman et al. 2022). The combination of soft bedrock, steep slopes, and soil toxicity that inhibits plant establishment and growth has resulted in runaway erosion and extensive areas of moonscape barrens (Alexander et al. 2007; Figure 10). All drainages of the New Idria serpentinite have very high natural sediment loads. Massive alluvium deposition and erosion occur along all stream channels during annual high rainfall events in winter and during rare monsoonal flash flood events in summer. Alluvium erosion and deposition is a constant, natural disturbance regime within the riparian zones (Figures 10–11). Plant species that grow within the riparian zones of the New Idria serpentinite are adapted to respond to this disturbance with rapid growth (stem and rhizome etiolation) up through the alluvium when buried (Figure 45). Additionally, there is recruitment of the species from seed dispersed onto the fresh, bare alluvium.

Ultramafic rock weathers to produce soils with chemically extreme properties that are adverse to plant establishment and growth of most plant species (Kruckeberg 1984, 2002; Alexander et al. 2007). Ultramafic soils are typically deficient in plant-essential nutrients including nitrogen, phosphorus, and potassium. The plant-essential soil calcium concentration is low (deficient) and magnesium is high (toxic), resulting in the key ultramafic soil character of low calcium:magnesium molar ratio (<<1). Additionally, plant-available nickel in the soil is often at toxic levels. Plants that can produce seed on ultramafic soils are physiologically adapted to the chemically extreme soil conditions. The plant populations may become isolated on the island-like areas of ultramafic rock, diverge genetically, and may speciate, becoming strict edaphic endemics (O'Dell & Rajakaruna 2011). *Castilleja benitoensis* is one of at least 17 strict ultramafic endemic species that are known to occur on the New Idria serpentinite (Safford & Miller 2020). *Camissonia benitensis*, *C. benitoensis*, *Fritillaria viridea*, *Layia discoidea*, *Pyrrocoma benitoana*, and *Solidago guiradonis* are all strict ultramafic endemic species that only occur on the New Idria serpentinite mass and nearby (< 5 km west) Laguna Mountain and Panther Peak serpentinite masses. Strict ultramafic endemic species that co-occur with *C. benitoensis* in the same riparian zone habitat (niche) include *P. benitoana, S. guiradonis*, and *Salix breweri* (Figures 11–18). *Castilleja benitoensis* almost always occurs intermingled with or

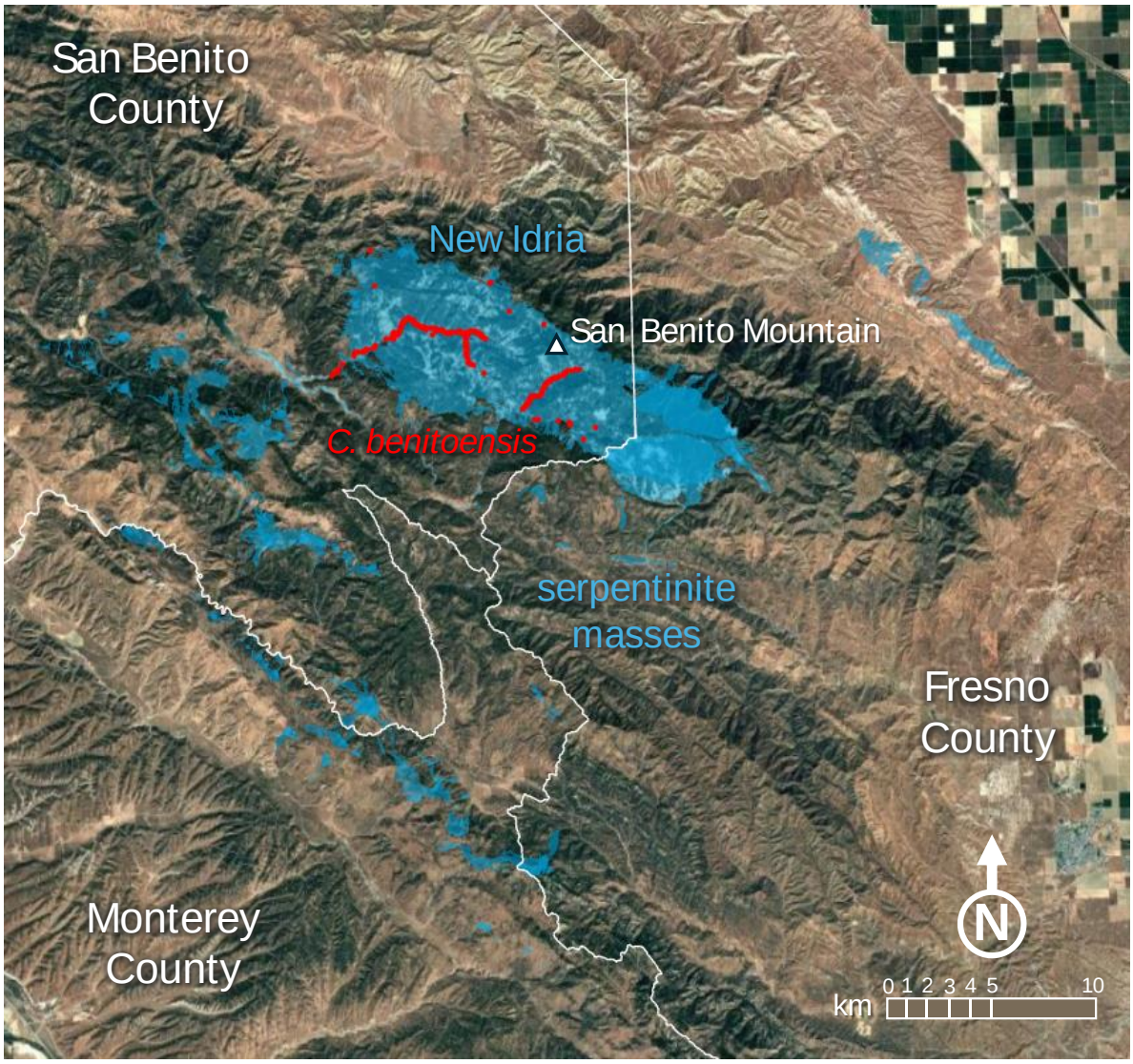
immediately adjacent to *S. breweri* and is almost certainly hemiparasitic primarily on that species, though *S. guiradonis* may sometimes be a secondary host. Despite the possibility of secondary hosts, the observed close relationship of *C. benitoensis* with *S. breweri* is remarkable among *Castilleja* species, approaching that of the almost obligate relationship between *Castilleja rigida* Eastw. and *Agave* species (primarily *A. lechuguilla* Torr.) in southwest Texas and adjacent northern Mexico (Egger et al. 2019).

We have observed no evidence of potential pollinator visitations to *Castilleja benitoensis*, though it is presumably pollinated by hummingbirds, based on the prominent red to red-orange coloration of the calyces and corollas and the long, tubular structure of the corollas, with both the stamens and pistils well-placed for pollen transfer during hummingbird visits for nectar extraction from the base of the corolla. There is some evidence of insect herbivory, likely from larvae, though such damage does not appear to be severe.

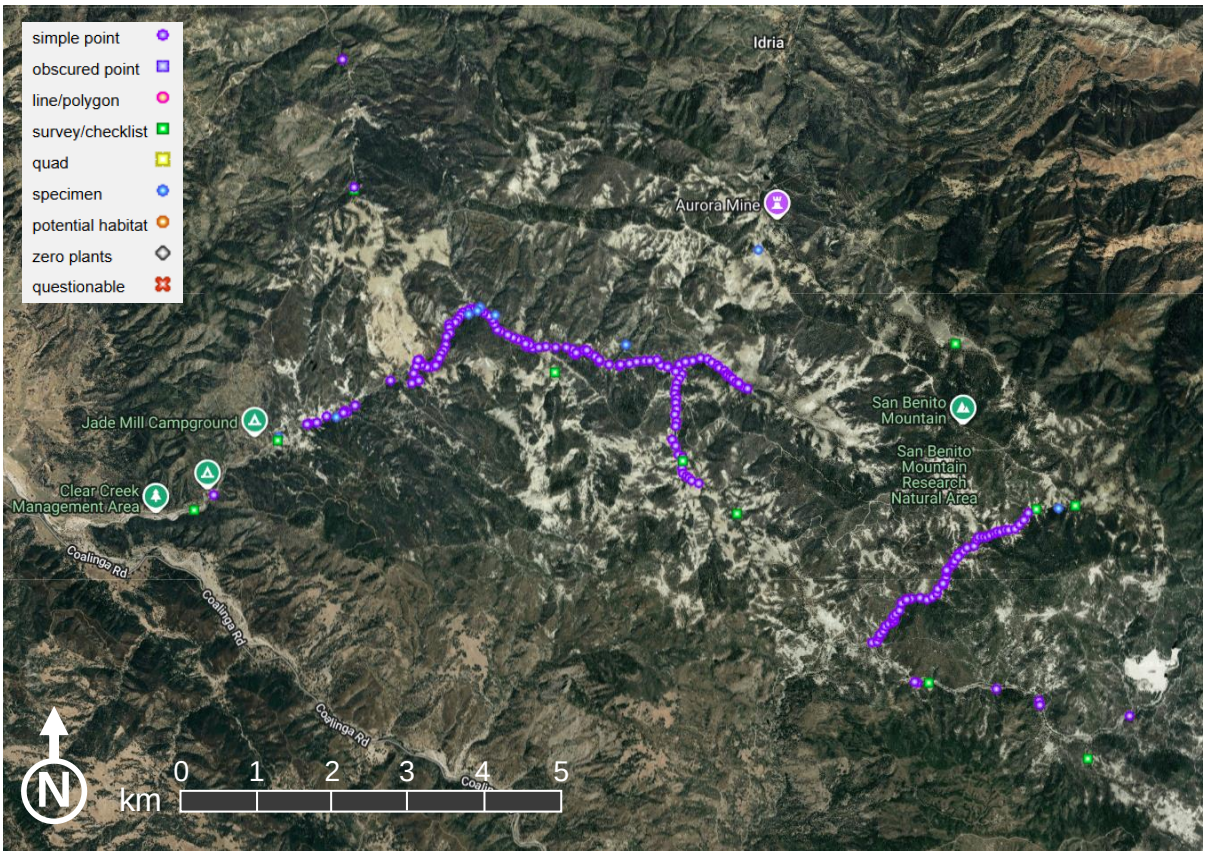
Rarity and conservation status. *Castilleja benitoensis* is an obligate wetland (riparian zone) species that occurs within the same habitat (niche) as two other perennial, local ultramafic endemic species, *Pyrrocoma benitoana* (see Nesom 2025) and *Solidago guiradonis.* All three species are subject to the same type, intensity, and frequency of natural disturbance in their shared riparian zone habitat. The alluvial processes within the riparian zone habitat are high intensity (massive alluvial deposition and erosion) and occur annually (winter rainfall high flow). There are occasional extreme intensity rainfall events that occur during El Niño winters and summer monsoonal storms, resulting in flash floods. All the riparian zone plant species are adapted to this disturbance regime.

Primary anthropogenic disturbance on the New Idria serpentinite from 1970 to 2008 was off-highway vehicle (OHV) travel (Griffin 1984; Coleman 1996). The New Idria serpentinite mass is designated as an Area of Critical Environmental Concern (ACEC) and located within Clear Creek Management Area, administered by the Bureau of Land Management (BLM). Clear Creek Management Area was closed to OHVs by the BLM in 2008. Although most of the historic OHV disturbance was likely within the background level of the natural disturbance regime experienced by the riparian zone species, that disturbance has been largely eliminated.

Solidago guiradonis has approximately the same small range as *Castilleja benitoensis* and *Pyrrocoma benitoana* and is locally common throughout the riparian zones of the New Idria serpentinite. A census conducted for *Solidago guiradonis* found at least 200,000 individuals (adults), with the total estimated to be as high as 400,000 individuals due to undercount of juveniles (Bureau of Land Management 2015, unpublished). The census data was provided to the California Native Plant Society (CNPS) Rare Plant Program. CNPS analyzed the data and concluded to maintain *S. guiradonis* at California Rare Plant Rank (CRPR) 4.3. Surveys for both *P. benitoana* and *C. benitoensis* throughout the New Idria serpentinite are not as complete as for *S. guiradonis*, but both species are known to occur within the major drainages of Clear Creek, Larious Creek, San Carlos Creek, Picacho Creek, Sawmill Creek, and upper San Benito River (Calflora 2026; iNaturalist 2026). The distribution and abundance of *C. benitoensis* and *P. benitoana* are similar in the areas that have been surveyed. Both species are sparsely scattered along perennial stream banks, with occasional higher density clusters in semi-stable areas of stream banks. Total number of individuals of *C. benitoensis* is estimated at 10,000. Total number of individuals of *P. benitoana* is estimated at 30,000. Both *C. benitoensis* and *P. benitoana* are substantially rarer than *S. guiradonis* and are subject to the same level of threat. Consequently, we propose a CRPR rank of 1B.3. CRPR 1B is defined as plants that are rare, threatened, or endangered in California and elsewhere. A threat level of 0.3 is defined as not very threatened in California with less than 20% of occurrences threatened/low degree and immediacy of threat, or no current threats known. Additionally, we recommend a NatureServe global rank of G3, Vulnerable, due to restricted range and habitat and relatively small numbers of individuals.



Map 1. Current known distribution of *Castilleja benitoensis*, indicated in red in the context of the New Idria serpentinite mass, and other serpentinite masses of the area, indicated in blue. The species appears to be restricted to the New Idria serpentinite, as a local strict ultramafic endemic. Although botanical surveys have been conducted on the larger serpentinite masses to the southwest and south of the New Idria serpentinite, including Laguna Mountain, Panther Peak, and Charlie Mountain, no individuals of *C. benitoensis* have been found at those locations. The mapped locations are a composite of herbarium locations and confirmed images posted on the Calflora website. While not mapped here, observer posts on the iNaturalist website strictly conform to the same distribution.



Map 2. Locations of verified herbarium specimens and documented field observations of *Castilleja benitoensis* as displayed in Calflora, as of April 2026. All but a small number of the field observations were obtained and posted by O'Dell.

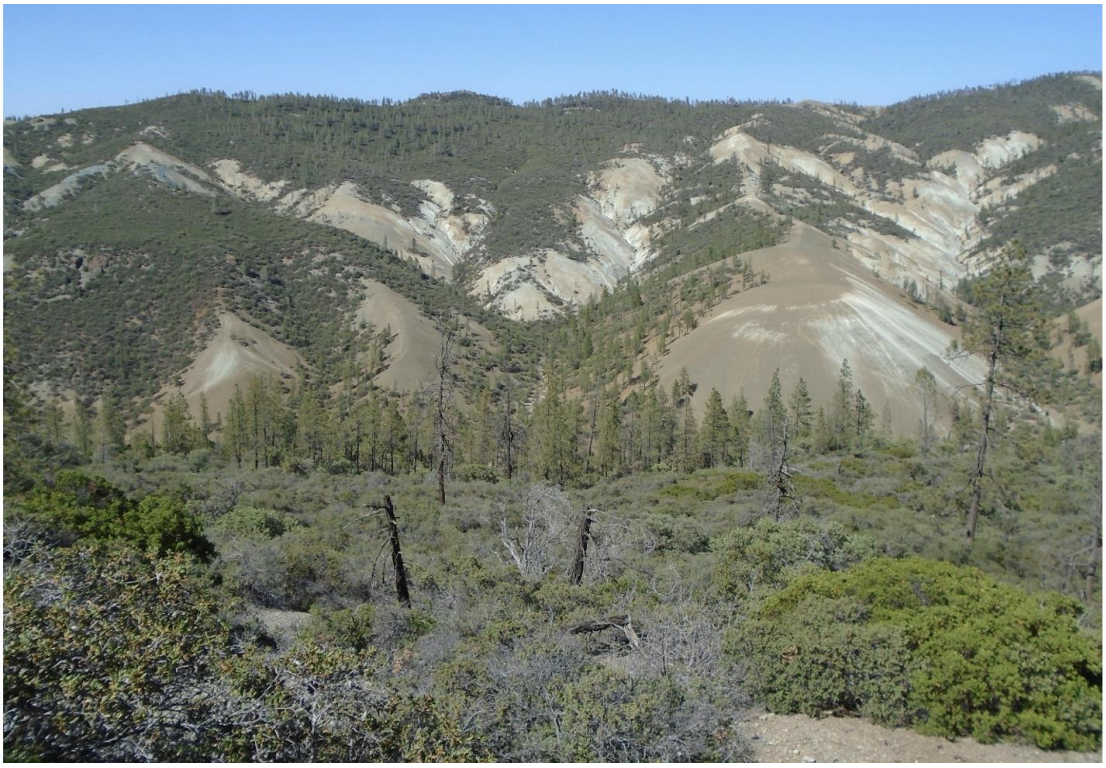


Figure 10a. Overview of the upper Clear Creek watershed within the New Idria serpentinite.

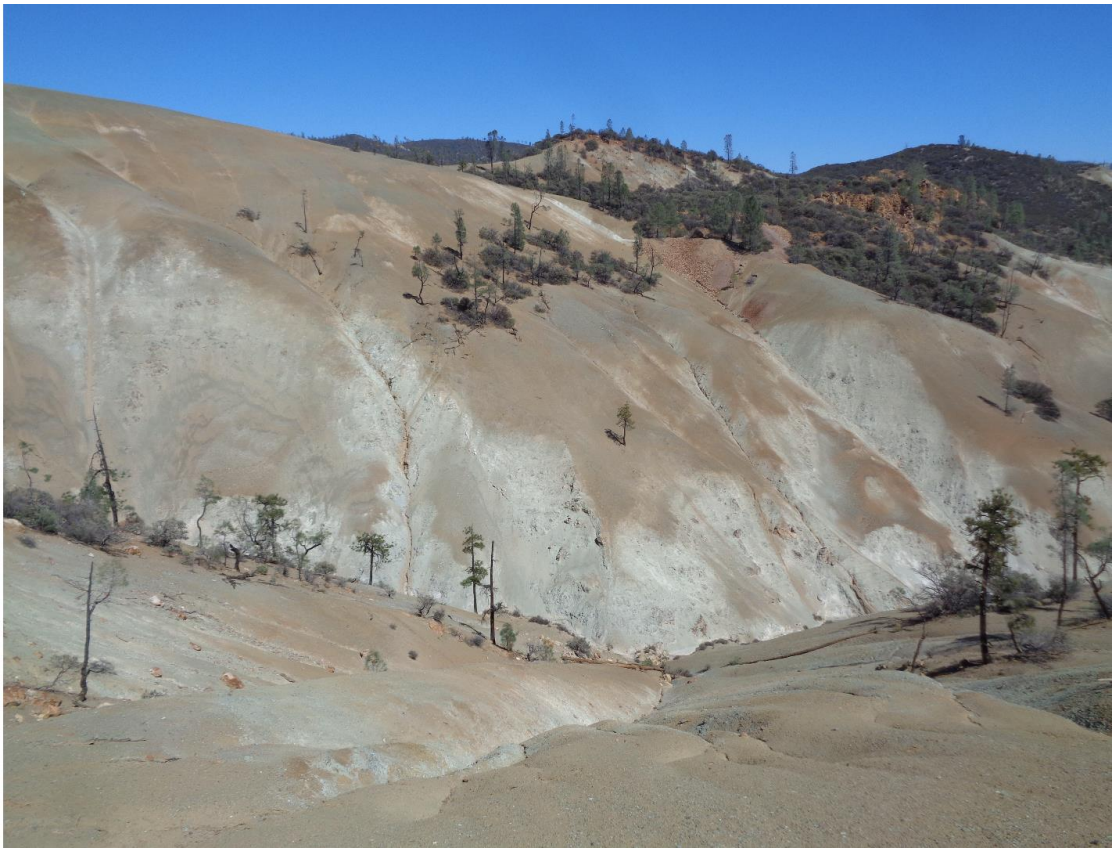


Figure 10b. Extensive, natural, erosive barrens are a unique feature of this landscape. Photos by O'Dell.

Figure 11. Typical habitat of *Castilleja benitoensis* along Clear Creek. Note the bright green *Solidago guiradonis*, upper right corner, and the gray-green *Salix breweri*, in the background. These three strict ultramafic endemic species, along with *Aquilegia eximia*, *Parnassia palustris*, *Helenium puberulum*, *Stachys pycnantha*, *Sisyrinchium bellum*, *Achillea millefolium*, *Agrostis exarata*, *Muhlenbergia asperifolia*, and *Elymus trachycaulus* are allied as the riparian zone perennial vegetation type on the New Idria serpentinite. Photo by O'Dell.

Taxonomic relationships and identification. *Castilleja miniata* is one of the most widespread, morphologically and ecologically complex, and emblematic of the North American *Castilleja* species. Its nomenclatural history is fraught with many synonyms, assigning and reassigning of infra-specific taxa, intergrading races, and continuing debate among plant taxonomists. There are also several population systems in regions outside of California that justify further study and possible recognition at the rank of either species or variety. In addition to what we recognize here as *C. miniata* and four closely related species in the California Floristic Province, other named species and varieties are found outside of California. The Californian species and morphologically similar and presumably closely related species and infraspecific taxa from elsewhere in western North America, form the *C. miniata* complex, representing a phylogenetic hypothesis for future study and testing. The members of this complex are generally characterized by perennial habit, tall, mostly ascending-erect stems that are glabrous or puberulent and eglandular below the inflorescence, mostly entire leaves, bracts and calyx lobes relatively long and mostly with acute to acuminate lobes, adaxial and abaxial calyx clefts subequal and longer than the laterals, relatively long corollas with the beaks roughly equal to or slightly shorter than the tube, and an affinity to at least vernally moist substrates. All species of the *C. miniata* complex are readily placed within subg. *Castilleja*, as defined by Chuang and Heckard (1991). In this paper, we address only the elements of the *C. miniata* complex occurring in California, as they relate to *C.*

benitoensis. It is not intended as a full taxonomic treatment of the complex in its entirety. In this framework we follow the nomenclature standardized in the Flora of North America (FNANM – Egger et al. 2019) and adopted by Plants of the World Online (POWO 2026), with one exception, that of *C. oblongifolia* (see below). We recognize that there are nomenclatural and taxonomic discrepancies between the FNA treatment, as modified here, and that of the most recent iterations of the Jepson Flora Project (Chuang & Heckard 1993; Wetherwax et al. 2026), and these are addressed below.

In our view, the *Castilleja miniata* complex in California includes *Castilleja miniata* (Figures 46–46), *C. oblongifolia,* recognized anew at the rank of species (Figures 50–55), *C. elata* (Figures 56–60), and *C. uliginosa* (Figures 61–63), in addition to *C. benitoensis*. Their ranges are largely allopatric to parapatric in California (Map 3). In contrast to the remarkable ecological and edaphic flexibility of the nominate form of *C. miniata*, *C. elata*, *C. uliginosa*, and *C. oblongifolia* exhibit features of isolation (edaphic specialization, hydrologic refugia), morphological divergence, and at least partial geographic disjunction from the rest of the *C. miniata* complex. *Castilleja elata* is endemic to the Josephine ultramafic mass and the Agness-Snow Camp Mountain ultramafic mass in northwestern California and southwestern Oregon, where it grows around perennial seeps, along stream banks, and in fens. *Castilleja uliginosa* was endemic to the hydrologic refugium freshwater seep of Pitkin Marsh in Sonoma County, California, but it is now thought to be extirpated in the wild. *Castilleja oblongifolia* is endemic to the Transverse Ranges and Peninsular Ranges of southern California, and southward to the Sierra Juarez of northern Baja California, Mexico, where it grows around perennial seeps and along stream drainages. Some populations occur on gabbro soil between Descanso and Julian in San Diego County. Conspicuous among the ranges of all these forms is the curiously disjunct and restricted distribution of *C. benitoensis* on the New Idria serpentinite in a portion of a single mountain range, where it grows around perennial seeps and along stream banks. *Castilleja benitoensis* is disjunct from any other known populations of *C. miniata* by at least 150 airline km.

The following is a summary and comparison of the nomenclature, ecology, and distribution of the members of the *Castilleja miniata* complex in California, as presented in the FNA and in the most recent update of the Jepson Flora Project (JFP). The bold-face names are those used in this paper and which we believe best represent the diversity of the *C. miniata* complex in the Californian Floristic Region.

Castilleja *miniata* Douglas ex Hook. var. *miniata* (FNA)
(subsp. *miniata* in JFP)
Ecology: Perennial stream banks, perennial seeps, wet to moderately dry meadows and slopes. No apparent edaphic affinity.
Köppen-Geiger climate: Csb warm summer mediterranean, Dsb warm summer mediterranean continental, Dsc dry summer subarctic; Dfb warm summer humid continental; ET tundra
Distribution (JFP): NW, CaR, SNH, c CCo, SCoRO, SW, GB.
Distribution (FNA): widespread in w North America (except near coast in most of California).

***Castilleja oblongifolia* A. Gray**
(Castilleja miniata var. oblongifolia (A. Gray) P.A. Munz in FNA)
(synonym of *C. miniata* subsp. *miniata,* JFP)
Ecology: Perennial stream banks, perennial seeps and adjacent hillsides. No apparent edaphic affinity. Some populations occur on gabbro soil between Descanso and Julian in San Diego County.
Köppen-Geiger climate: Csb warm summer mediterranean, Dsb warm summer mediterranean continental, Dsc dry summer subarctic
Distribution (FNA): Cuyamaca, Laguna, San Bernardino and e San Gabriel mountains of sw California southward to the Sierra Juarez of northern Baja California.

Castilleja elata Piper (FNA).
(*C. miniata* subsp. *elata* (Piper) T.I. Chuang & Heckard in JFP)
Ecology: Perennial stream banks, perennial seeps, fens ("bogs"). Ultramafic Broad Endemic (Safford and Miller 2020). Endemic to the Josephine ultramafic mass and Agness-Snow Camp Mountain ultramafic mass.
Köppen-Geiger climate: Csb warm summer mediterranean
Distribution (JFP): nw KR
Distribution (FNA): NW California and SW Oregon.

Castilleja uliginosa Eastw. (FNA)
(synonym of *C. miniata* subsp. *miniata* in JFP)
Ecology: Wet meadows, freshwater marsh. No apparent edaphic affinity.
Köppen-Geiger climate: Csb warm summer mediterranean
Distribution (FNA): Pitkin Marsh, Sonoma County (extirpated in the wild).

Castilleja benitoensis J.M. Egger & R.E. O'Dell
Ecology: Perennial stream banks, perennial seeps. Ultramafic Strict Endemic. New Idria serpentinite and serpentinite alluvial deposits of perennial creeks downstream.
Köppen-Geiger climate: Csa hot summer mediterranean (barely), Csb warm summer mediterranean (primary, core range)
Distribution: San Benito Mountain. SCoRI. San Benito County (and likely in closely adjacent parts of Fresno Co.); central California.

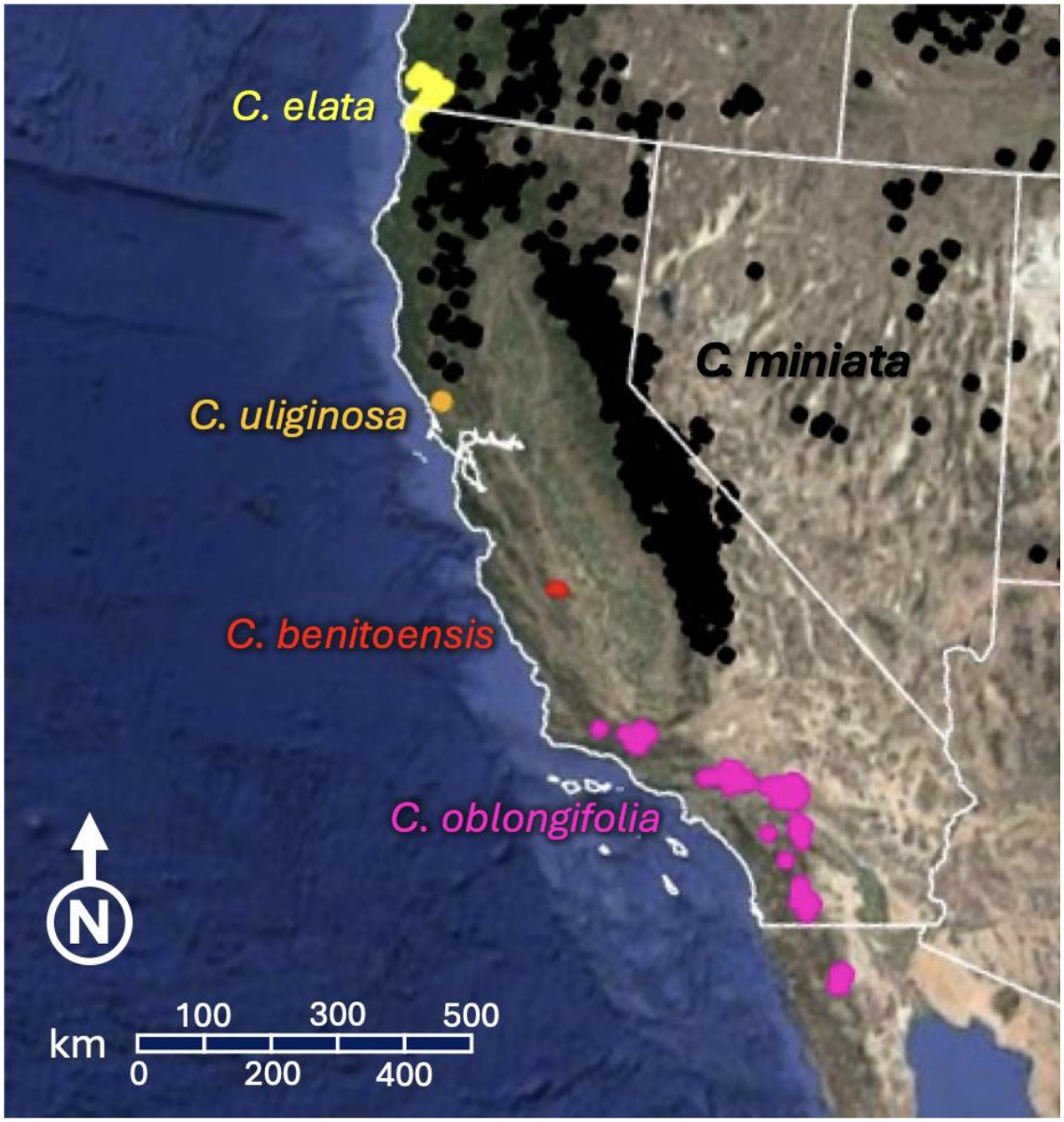
KEY TO THE *CASTILLEJA MINIATA* COMPLEX IN CALIFORNIA

1. Bracts pale yellow to cream, sometimes greenish proximally; formerly endemic to wet meadows of the Pitkin Marsh, Sonoma County, now considered extirpated in the wild ……..... **Castilleja uliginosa**
1. Bracts brightly colored, only rarely if ever pale yellow to cream; plant not occurring in or adjacent to Sonoma County.

2. Bracts at least distally pink-purple, magenta, or reddish-purple, sometimes buff to dull yellow-orange; serpentine bogs and wetlands; Siskiyou Mountains, Del Norte and adjacent Siskiyou counties and adjacent southwest Oregon ……..…..…….. **Castilleja elata**
2. Bracts at least distally usually red to red-orange, though a wide range of occasional color variants occur in var. *miniata*; plants absent from northern California except var. *miniata* and then not found in serpentine bogs and wetlands and mostly absent from the range of *C. elata.*

3. Distal stem leaves usually inconspicuous and reduced; stems and leaves uniformly densely strigillose-puberulent; bracts reduced, weakly and gradually differentiated from the leaves, and only the distal ones brightly colored, contributing little to the bright coloration of the inflorescences, that provided mostly by the conspicuously colored calyces and corollas; corolla beaks usually uniformly brightly colored; bracts almost always entire; plants strongly rhizomatous, often forming complex rooting masses; strictly limited to serpentinite alluvial deposits along perennial streams in the vicinity of San Benito Mountain (New Idria serpentinite mass) ……..……. **Castilleja benitoensis**
3. Distal stem leaves usually conspicuous and well-developed; stems and leaves usually glabrous-glabrescent (*C. miniata*) to puberulent (*C. oblongifolia*); all but the most proximal bracts fully developed, well differentiated from the leaves, and conspicuously colored, significantly contribution to inflorescence coloration; bract lobes 1–5(–7), all but most proximal bracts usually divided; corolla beaks usually greenish to stramineous adaxially with brightly colored margins; plants not at all to weakly rhizomatous with proximal stems sometimes decumbent and rooting; occurring in a wide range of moist to moderately dry habitats (except *C. oblongifolia*) and without apparent edaphic affinities; absent from the coastal mountains of west-central California.

4. Stems glabrous to glabrate proximally, densely puberulent medially and distally; distal leaves appressed-ascending, ascending, or spreading, often thickened and coarse-textured; calyx lobe apices linear-acuminate; Cuyamaca, Laguna, San Bernardino and eastern San Gabriel mountains of southwestern California (rarely in the Sespe region of Ventura County), south to the Sierra Juarez of northern Baja California, Mexico …….. **Castilleja oblongifolia**
4. Stems usually glabrous to glabrate or sometimes sparsely pubescent, with spreading to weakly appressed hairs; distal leaves thin or sometimes coarse-textured, usually spreading to ascending; calyx lobes linear to lanceolate, with blunt to acuminate apices; widespread western North America but not in the range of *C. oblongifolia* except for some mixing of traits in the San Gabriel Mountains and southern Sierra Nevada ……...……. **Castilleja miniata**



Map 3. Distribution of members of the *Castilleja miniata* complex occurring in California. *Castilleja miniata* (black), *C. oblongifolia* (pink), *C. elata* (yellow), *C. uliginosa* (orange), and *C. benitoensis* (red). The ranges *Castilleja miniata* and additional forms in the *C. miniata* complex extend far to the north and east of the map area, into Canada and Alaska.

Field photographs and herbarium specimens illustrating the distinctive characters of *C. benitoensis* are presented below in Supplemental images, parts 1–2 (Figures 19–45). Holotype specimens and representative field photographs of the other components of the *Castilleja miniata* complex in California are presented below in Supplemental images, parts 3–5 (Figures 46–63).

Within the *Castilleja miniata* complex, *C. benitoensis* is morphologically and geographically most aligned with *C. oblongifolia*. The latter, which only occasionally has oblong leaves (Figures 50–52), occurs in the southern South Coast Ranges, Transverse Ranges, and Peninsular Ranges of southern California and in the Sierra Juarez of adjacent northern Baja California, and it shares some characters with *C. benitoensis* that are found only occasionally in *C. miniata*. These include the striking calyx structure, with very long, linear-acuminate, often spreading lobes, puberulent stems and leaves, and a tendency toward appressed distal leaves, though the latter trait is most conspicuous in *C. benitoensis*. The two differ in most characters in the key, as well as in the disjunction and edaphic and ecological specialization of *C. benitoensis*. It is reasonable to hypothesize that *C. benitoensis* arose from *C. oblongifolia* or a common ancestor due to either long-distance dispersal or isolation and disjunction from a previously more contiguous distribution, followed by adaptation to the extreme environment to which it has since become endemic. Gray's original concept of *C. oblongifolia* was based on one of three specimens collected by Palmer (Figure 50) and mounted together on the holotype sheet, with a notation, "the left-hand sp. unique", and only the left-most of the three stems on the sheet fully matches the description of the type (Gray 1878, p. 296). The other two specimens on the sheet lack the highly oblong leaves of the third stem and are superficially more like typical *C. miniata*. Gray's protologue also states that the type was "collected along with *C. miniata*". However, *C. oblongifolia* is best understood as being unique from *C. miniata* in features other than the oblong leaves of Gray's single stem, and, using a more complete listing of the unique characters of this form, all stems of Palmer's collection on the holotype sheet are typical of the more broadly interpreted *C. oblongifolia*.

Other examples exist in *Castilleja* of species groups consisting of a relatively widespread species and morphological similar species that have apparently become established in disjunct locations with differing ecological and edaphic conditions and have accumulated significant morphological differences as well, perhaps representing an example of the Founder Effect and genetic drift. One such example also represented in the California flora is that of *Castilleja ambigua* Hook. & Arn., a wide-ranging coastal species of salt marshes and adjacent sandy bluffs and low dunes ranging from the central coast of California north to southern Vancouver Island, Canada. While there is some morphological variation in *C. ambigua*, such as that represented by var. *insalutata* (Jeps.) J.M. Egger primarily in Monterey County and var. *humboldtiensis* (D.D. Keck) J.M. Egger in Humboldt and Mendocino counties, they are all similar in general morphology and strict-coastal distribution. On the other hand, two recently recognized, but related species, *C. meadii* (Egger et al. 2012, 2025) and *C. heckardii* (Egger & Excoffier 2021, Egger et al. 2025), have adapted to different, localized, restrictive habitats and have accumulated more substantial morphological differences.

ACKNOWLEDGEMENTS

We thank David E. Giblin (WTU) for a critical reading of the manuscript, Kanchi N. Gandhi (GH) for nomenclatural advice, and Kristen Nelson for use of her photograph (Figure 45). We also express our gratitude to the staff of the following herbaria for assistance with and use of their holdings and specimen images: CAS, GH, K-BENTH, NY, UC/JEPS, WTU.

LITERATURE CITED

Alexander, E.B., R.J. Coleman, T. Keeler-Wolf, S. Harrison. 2007. Serpentine geoecology of western North America. Oxford Univ. Press.

Beck, H.E., N.E. Zimmermann, T.R. McVicar, N. Vergopolan, A. Berg, N.J. Lutsko, A. Dufour, Z. Zeng, X. Jiang, A.I.J.M. van Dijk, and D.G. Miralles. 2023. High-resolution (1 km) Köppen-

Geiger maps for 1901–2099 based on constrained CMIP6 projections. Scientific Data 10. <DOI:10.1038/s41597-023-02549-6>

Bureau of Land Management. 2015. Central Coast Field Office (formerly Hollister Field Office). BLM Clear Creek Management Area *Solidago guiradonis* census. Visual survey conducted October 24–November 1, 2013. Watersheds surveyed included Larious Creek, Clear Creek, San Carlos Creek, Sawmill Creek, Upper San Benito River, Canada Azul, Arroyo Leona, and White Creek. Total individuals counted = 200,221.

Chuang, T.I and L.R. Heckard. 1991. Generic realignment synopsis of Subtribe Castillejinae (Scrophulariaceae – Tribe Pedicularеae). Syst. Bot. 16_644–666.

Chuang, T.I and L.R. Heckard. 1993. *Castilleja*. Pp. 1016–1024, in J.C. Hickman (ed.). The Jepson Manual. Higher Plants of California, 1st ed. Univ. of Calif. Press, Berkeley.

Calflora. 2026. The Calflora Database (Calflora). Berkeley, California. <Calflora.org> Accessed 18 Jan 2026.

Consortium of California Herbaria 2 (CCH2) Portal. 2026. Berkeley, California. <cch2.org> Accessed: 18 Jan 2026.

Coleman, R.G. 1996. New Idria serpentinite: A management dilemma. Environmtl Engin. Geosci. 2: 9–22.

Coleman, R.G., J.T. Gooley, R.T. Gregory, S.A. Graham. 2022. New Idria serpentinite protrusion, Diablo Range, California: From upper mantle to the surface. Amer. J. Sci. 322: 533–560. <DOI:10.2113/gssgfbull.II.6.961>

Egger, J.M., J.A. Ruygt, and D.C. Tank. 2012. *Castilleja ambigua* var. *meadii* (Orobanchaceae): A new variety from Napa County, California. Phytoneuron 2012-68: 1–12.

Egger, J.M., P.F. Zika, B.L. Wilson, R.E. Brainerd, and N. Otting. 2019. *Castilleja.* Pp. 565–665, in Flora of North America Editorial Committee (eds). Flora of North America North of Mexico, Vol. 17.

Egger, J.M. and P. Excoffier. 2021. *Castilleja ambigua* var. *heckardii* (Orobanchaceae): A new variety from San Luis Obispo County, California. Phytoneuron 2021-15: 1–17.

Egger, J.M., P. Excoffier, and J.A. Ruygt. 2025. Elevation to species rank of two range-restricted varieties of *Castilleja ambigua* (Orobanchaceae) from California. Phytoneuron 2025-53: 1–3.

Griffin J. 1984. San Benito Mountain. Fremontia 11: 22–23.

Gray, A. 1878. Synoptical Flora of North America, Vol. 2, part 1 (Gamopetalae after Compositae). Ivison, Blakeman, Taylor, and Co., New York.

iNaturalist. 2026. iNaturalist. California. <inaturalist.org> Accessed Jan 18, 2026.

Nesom, G.L. 2025. Taxonomy of the *Pyrrocoma racemosa* group (Asteraceae: Astereae). Phytoneuron 2025-08: 1–64.

Kruckeberg, A.R. 1984. California Serpentines: Flora, Vegetation, Geology, Soils and Management Problems. Univ. of California Press.

Kruckeberg, A.R. 2002. Geology and Plant Life: The Effects of Landforms and Rock Types on Plants. Univ. of Washington Press.

O'Dell, R.E. and N. Rajakaruna. 2011. Intraspecific variation, adaptation, and evolution. Pp. 97–137. in S.P. Harrison and N. Rajakaruna (eds.). Serpentine: Evolution and Ecology in a Model System. Univ. of California Press.

Plants of the World online (POWO). 2026. <https://powo.science.kew.org> Accessed 26 Apr 2026.

Remote Automated Weather Stations (RAWS). 2026. USA Climate Archive Stations: Marquez California, Santa Rita California. <https://raws.dri.edu/> Accessed Jan 18, 2026.

Safford, H. and J.E.D. Miller. 2020. An updated database of serpentine endemism in the California flora. Madroño 67: 85–104. <DOI:10.3120/0024-9637-67.2.85>

Wetherwax, M., T.I. Chuang, and L.R. Heckard. 2026. *Castilleja*, in Jepson Flora Project (eds.) *Jepson eFlora*, Revision 14. <https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=11347> Accessed April 16, 2026.

Supplemental images, part 1. Photos of *Castilleja benitoensis* from the vicinity of the type locality in the Sawmill Creek drainage from 2023–2025 in areas where riparian community structure is fully developed. Photos by Egger except where noted.

Figure 12. *Castilleja benitoensis* at the type locality along Sawmill Creek, 8 September 2025, along with its likely host species, *Salix breweri* (lanceolate, gray-green leaves), and another close associate, *Solidago guiradonis*. All three species are strict serpentinite endemics.

Figure 13. Two views of the well-developed riparian community at the type locality along Sawmill Creek, 8 September 2025. Dominant plants in this community include *Castilleja benitoensis* (lower center-right), its likely host species, *Salix breweri*, as well as *Solidago guiradonis*, and *Aquilegia eximia* (lower far right) All four species are strict serpentinite endemics.

Figure 14. Typical riparian community structure at the type locality along Sawmill Creek, 8 September 2025. Dominant plants in this community include *Castilleja benitoensis*, along with its likely host species, *Salix breweri* and *Solidago guiradonis*.

Figure 15. The long stems of *Castilleja benitoensis*, while upright-ascending at first, often sprawl over or among the relatively low stems of *Salix breweri*. Along Sawmill Creek, 8 September 2025.

Figure 16. *Castilleja benitoensis* and its apparent primary host, *Salix breweri*. Along Sawmill Creek, 8 September 2025.

Figure 17. Riparian zone in the bed of Sawmill Creek, showing the sharp transition from the *Salix-Castilleja-Solidago* community of the perennially moist subsoil to the drier *Arctostaphylos-Pinus* community on the hillsides above, 8 September 2025.

Figure 18. *Castilleja benitoensis* with two frequent serpentinite-endemic associates, Solidago *guiradonis* and *Aquilegia eximia*. Along Sawmill Creek, 8 September 2025.

Figure 19. *Castilleja benitoensis*, inflorescences at full anthesis, along Sawmill Creek, 8 September 2025. Note the ripe pollen grains in the uppermost corolla and the spent anthers pendently exserted from the corolla beak on the lower two flowers of the same stem.

Figure 20. *Castilleja benitoensis*, closeup of inflorescence at full anthesis, along Sawmill Creek, 8 September 2025. Note the ripe pollen grains in the uppermost corolla and the spent anthers pendently exserted from the corolla beak on the lower two flowers of the same stem.

Figure 21. *Castilleja benitoensis*, closeup of inflorescence at full anthesis, along Sawmill Creek, 8 September 2025.

Figure 22. *Castilleja benitoensis*, abaxial view of a prominent flower, along Sawmill Creek, 8 September 2025. Note the deep calyx lobes spreading widely from the prominent corolla.

Figure 23. A two-flowered inflorescence of *Castilleja benitoensis*, showing the reduced, entire bracts and prominent calyces and corollas, as well as the mixed pilosulose and stipitate-glandular puberulence of these flower parts. Along Sawmill Creek, 8 September 2025.

Figure 24. *Castilleja benitoensis*, inflorescence showing the transition from the strigillous stem pubescence to the longer mixed villous and shorter, stipitate-glandular pubescence of the inflorescence, along Sawmill Creek, 8 September 2025. Also note the very deep lateral calyx cleft and long-acuminate lobes in the upper left flower.

Figure 25. *Castilleja benitoensis*, closeup showing the pubescence of the inflorescence with its mixture of eglandular-villous and shorter, stipitate-glandular hairs, along Sawmill Creek, 8 September 2025.

Figure 26. Upper stem and inflorescence of *Castilleja benitoensis*, along Sawmill Creek, 8 September 2025. Note the gradual transition from the typically reduced and appressed upper stem leaves to the increasingly acuminate and brightly colored but still entire and relatively inconspicuous floral bracts.

Figure 27. A portion of the lower-distal stem and leaves of *Castilleja benitoensis*, showing the typical strigillous pubescence and somewhat appressed leaf position. Also note the strongly anthocyanic coloration found in some plants of this species. Along Sawmill Creek, 8 September 2025.

Figure 28. Freshly collected rhizomatous root mass of *Castilleja benitoensis*, Sawmill Creek drainage, 26 October 2023, part of *O'Dell s.n.*, now deposited at WTU. Photo by O'Dell.

Figure 29. Freshly collected rhizomatous root mass of *Castilleja benitoensis*, Sawmill Creek drainage, 26 October 2023, part of *O'Dell s.n.,* now deposited at WTU. Photo by O'Dell.

Figure 30. Rhizomatous root masses of *Castilleja benitoensis*, Sawmill Creek drainage, 26 October 2023, *O'Dell s.n.*, sheet H, WTU.

Figure 31. Rhizomatous root masses of *Castilleja benitoensis*, Sawmill Creek drainage, 26 October 2023, *O'Dell s.n.*, sheet G, WTU.

Figure 32. *Castilleja benitoensis*, Sawmill Creek drainage, 26 October 2023, *O'Dell s.n.*, sheet A, distal portion, WTU.

Figure 33. *Castilleja benitoensis*, Sawmill Creek drainage, 26 October 2023, *O'Dell s.n.*, sheet A, proximal portion, WTU.

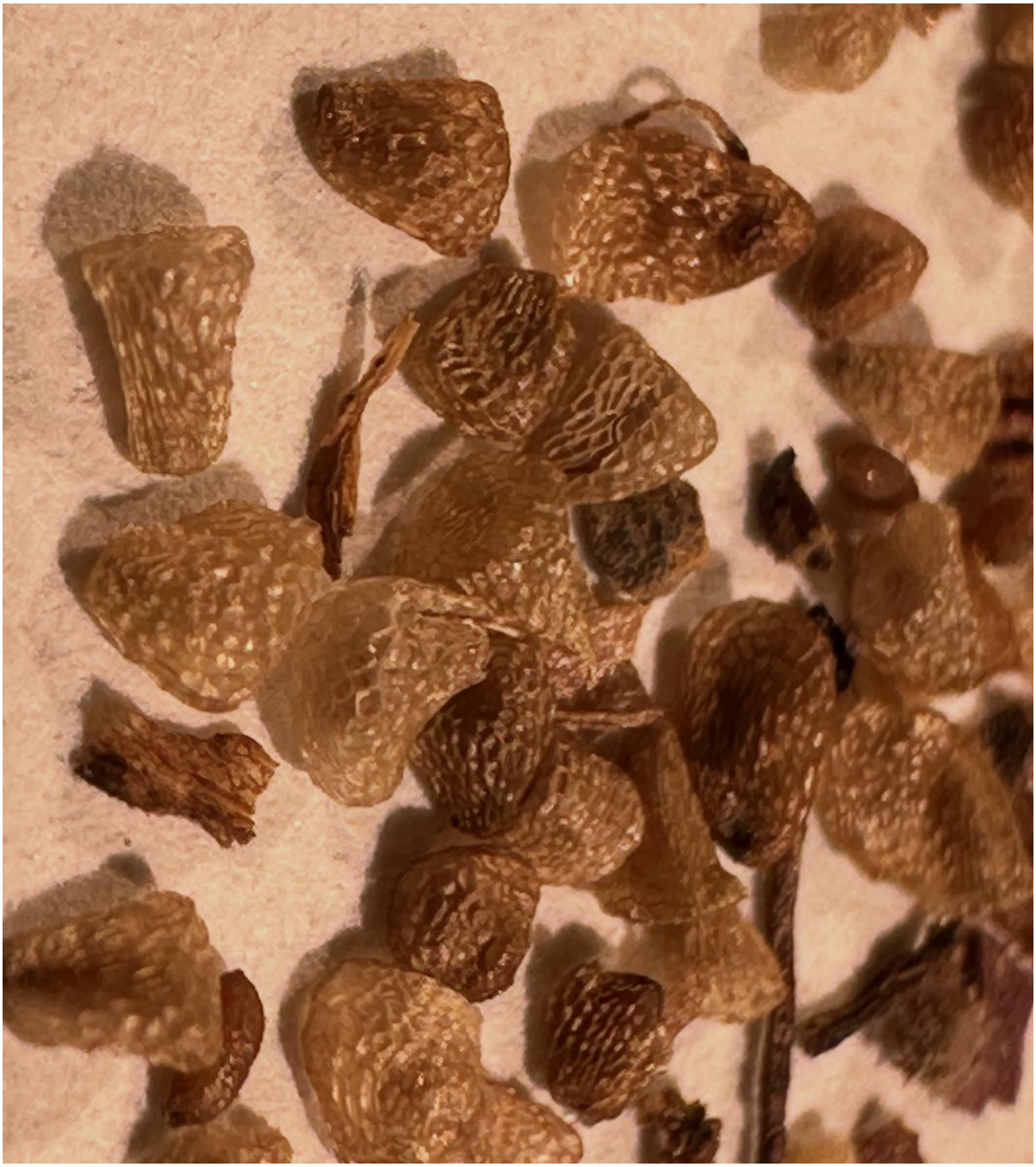


Figure 34. Seeds of *Castilleja benitoensis* from type collection. Note the loose-fitting, unruptured seed coats and shallow reticulations. The seeds range from 1–2.5 mm along the longest axis.

Figure 35. First collection of *Castilleja benitoensis*, 20 July 1861, *W.H. Brewer 772*, UC, duplicates at GH and US. Brewer went up to the mines on San Carlos Peak, barely into the New Idria serpentinite at a small pond/lake at San Carlos Creek, where this specimen was likely collected. The type specimen of *Solidago guiradonis* was also collected there.

Supplemental images, part 2. Photos from the Clear Creek drainage from 2022–2025 in areas heavily affected by flood waters from major rain events during the winter of 2021–2022. Photos by Egger except where noted.

Figure 36. *Castilleja benitoensis* with *Pyrrocoma benitoana* in the background, another endemic species of the New Idria serpentinite. Along Clear Creek, 8 September 2025.

Figure 37. *Castilleja benitoensis* with *Salix breweri*, another serpentinite endemic and primary host for the *Castilleja*, along Clear Creek, 8 September 2025. Upper image shows the creek side habitat with the plants in the lower image appearing in the lower right foreground.

Figure 38. *Castilleja benitoensis* on banks of Clear Creek, stems emerging from depauperate *Salix breweri*, 18 October 2023. Photo by O'Dell.

Figure 39. *Castilleja benitoensis* on banks of Clear Creek, stems emerging from depauperate *Salix breweri*, 18 October 2023. Note that even during the late summer, after six months of no rain as typical for this Mediterranean climate, there is still strong surface flow in Clear Creek. Year-round (perennial) strong surface flow is a common feature of the streams on the New Idria serpentinite mass, but uncommon for streams of the nearby mountains. Average annual rainfall of the region is highest (~500 mm) on San Benito Mountain (elev. 1605 m). Most rainfall occurs during the winter. The rain infiltrates the pulverized serpentinite rock in winter and then seeps out at low points along the drainages the rest of the year. Photo by O'Dell.

Figure 40. *Castilleja benitoensis* inflorescence, along Clear Creek, 8 September 2025. Note the reduced, undivided bracts, the linear-acuminate and spreading calyx lobes, and long, uniformly reddish corolla beaks, as well as the few-flowered inflorescence itself. While some inflorescences in this species continue developing and lengthening, it is common for plants to produce many smaller inflorescences from the same central stem.

Figure 41. *Castilleja benitoensis* inflorescence, along Clear Creek, 8 September 2025. Note the reduced, undivided bracts, the linear-acuminate and spreading calyx lobes, and long, uniformly reddish corolla beaks, as well as the few-flowered inflorescence itself. While some inflorescences in this species continue developing and lengthening, it is common for plants to produce many smaller inflorescences from the same central stem.

Figure 42. *Castilleja benitoensis*, along Clear Creek, 8 September 2025. Somewhat depauperate plant growing in crevice of serpentinite rock and without an apparent nearby host plant. Also note the unusual anthocyanic coloration of the stems and leaves.

Figure 43. *Castilleja benitoensis*, close-ups of leaves and pubescence of distal stems. In the lower photo, of the middle portion of the distal stem half, note the dense but minute strigillose pubescence. This pubescence essentially coats the entire plant below the inflorescence. In the upper photo, note the transition from left to right from the strigillose, eglandular stem pubescence to the mixed pubescence of the inflorescence, consisting of longer pilosulose and shorter stipitate-glandular hairs. Also note in both images the reduced, almost scale-like leaves of the distal stems, along with their often-apiculate tips. Along Clear Creek, 8 September 2025.

Figure 44. *Castilleja benitoensis*, close-ups of leaves and pubescence of proximal stems. Note the dense but minute strigillose pubescence. This pubescence essentially coats the entire plant below the inflorescences. Along Clear Creek, 8 September 2025.

Figure 45. Early regenerative growth of *Castilleja benitoensis* from the subterranean rhizomatous root mass following severe flooding during the winter of 2021–2. Clear Creek drainage, 24 April 2022. Photo by Kristen Nelson, iNaturalist post 112792208.

Supplemental images, part 3. Photos of *Castilleja miniata* var. *miniata*. Photos by Egger.

Figure 46. Lectotype of *Castilleja miniata*, *Douglas s.n.*, Blue Mountains, 1826 (K-BENTH). The lectotypification was published by F.W. Pennell (Proc. Acad. Nat. Sci. Phila 86: 539, 1934).

Figure 47. *Castilleja miniata* var. *miniata*, SW of Tollgate, NW Blue Mountains, Union County, Oregon, 19 July 2023. Note the glabrous stems and well-developed distal leaves, as well as the prominent, divided bracts.

Figure 48. *Castilleja miniata* var. *miniata*, SW of Tollgate, NW Blue Mountains, Union County, Oregon, 19 Jul 2023. Note the prominent, deeply divided bracts and the minute, granular excrescence found in the inflorescences of many plants of the nominate variety.

Figure 49. *Castilleja miniata* var. *miniata*, along Pacific Crest Trail near Frog Lake, Alpine County, California, 12 Jul 2024. Note the prominent, deeply divided bracts.

Supplemental images, part 4. Photos of *Castilleja oblongifolia*, by Egger.

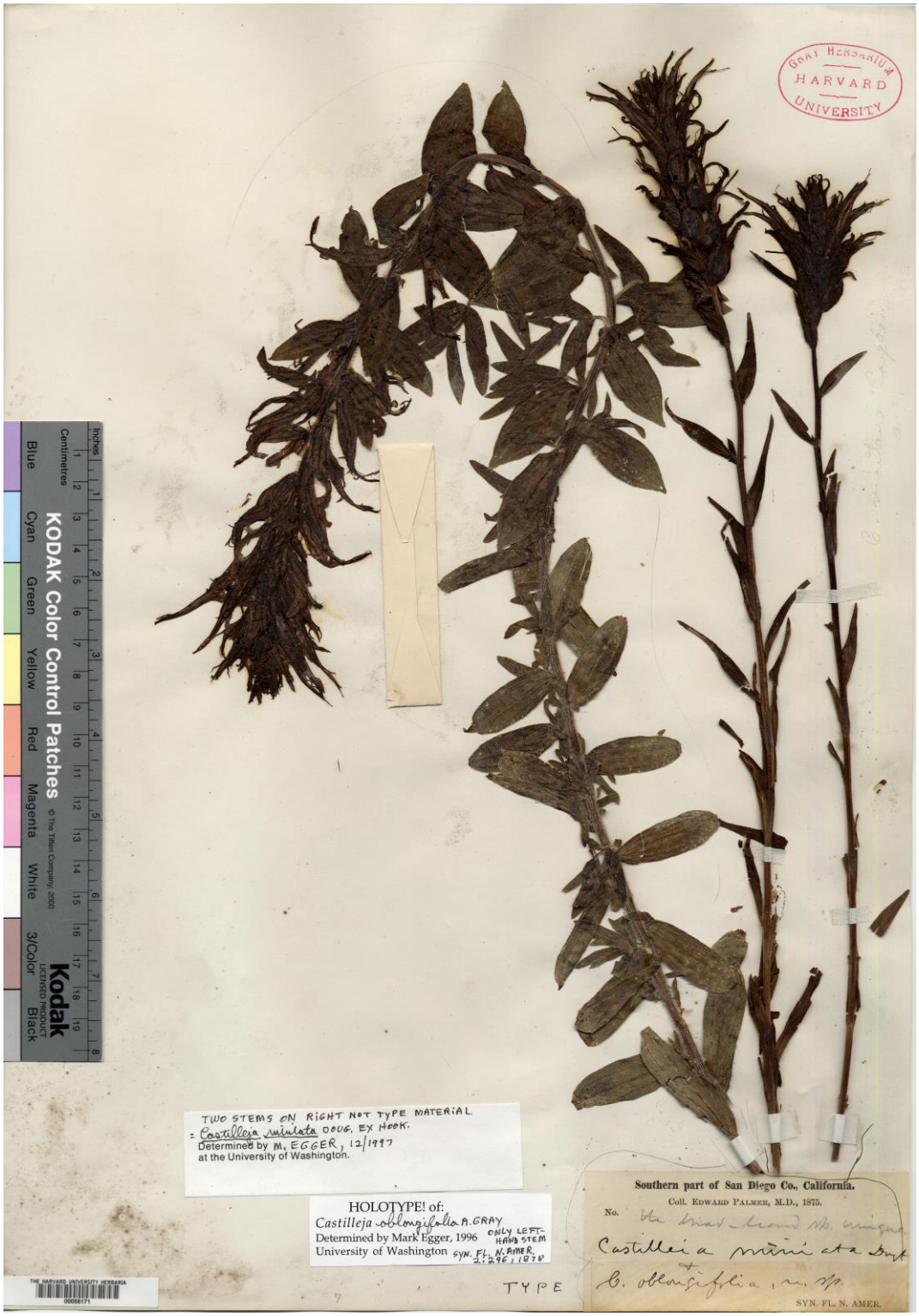


Figure 50. Holotype of *Castilleja oblongifolia* A. Gray, *Palmer s.n.*, southern part of San Diego County, California, Jul 1875 (GH). It has also been treated as *C. miniata* var. *oblongifolia* (A. Gray) P.A. Munz. While Gray treated only the left-hand stem as the type, we regard all the plants of the southern coastal ranges as this form, distinguished by traits other than the oblong leaves of the holotype.

Figure 51. *Castilleja oblongifolia*, Wildhorse Meadow Rd., San Bernardino County, California, 3 Jul 1997, *M. Egger 876b*, WTU. This specimen shows the range of leaf shapes found in *C. oblongifolia*, all expressed in a single, branching stem. Also see Figure 52.

Figure 52. *Castilleja oblongifolia*, seep area along Wildhorse Meadows Rd., San Bernardino Mountains, San Bernardino County, California, 3 July 1997. This is the same plant collected and preserved as *M. Egger 876b*, WTU in Figure 51 above.

Figure 53. *Castilleja oblongifolia*, Deer Lick Ranger Station, San Bernardino Mountains, San Bernardino Co., CA, 26 Jun 1992.

Figure 54. *Castilleja oblongifolia*, near Cuyamaca Reservoir, Cuyamaca Mountains, San Diego County, California, 20 July 2008.

Figure 55. *Castilleja oblongifolia*, near Cuyamaca Reservoir, Cuyamaca Mountains, San Diego County, California, 20 July 2008.

Supplemental images, part 5. Photos of *Castilleja elata.* Photos by Egger.

Figure 56. Holotype of *Castilleja elata* Piper, 8 mi. south of Waldo, Josephine County, Oregon, 14 Jun 1904, *Piper 5097* (US).

Figure 57. *Castilleja elata*, variations in common pink/violet/magenta form, E of O'Brien, Siskiyou Mountains, Josephine County, Oregon, 28 June 1991, *Egger 406* (WTU).

Figure 58. *Castilleja elata*, common pink/violet/magenta form, E of O'Brien, Siskiyou Mountains, Josephine County, Oregon, 28 June 1991, *Egger 406* (WTU). Note the *Darlingtonia californica* in the background, a frequent associate of this serpentine bog endemic.

Figure 59. *Castilleja elata*, common pink/violet/magenta form, E of O'Brien, Siskiyou Mountains, Josephine County, Oregon, 28 June 1991, *Egger 406* (WTU). Note the often shorter and acute but not acuminate bract and calyx tips and the modestly shorter corollas than in most *C. miniata*.

Figure 60. *Castilleja elata*, uncommon yellow-orange form, 1 mi. N of Gasquet, Siskiyou Mountains, Del Norte County, California, 28 Jun 1991, *Egger 408* (WTU). Note the often shorter and acute but not acuminate bract and calyx tips and the modestly shorter corollas than in most *C. miniata*.

Supplemental images, part 3. Photos of *Castilleja uliginosa*. Credits on each photo.

Figure 61. Holotype of *Castilleja uliginosa* Eastw., Pitkin Marsh, Sonoma County, California, 6 June 1937, *J.T. Howell 13031* (CAS).

Figure 62. *Castilleja uliginosa*, last specimen of this species known to exist in the wild. It died sometime in the late 1980s. Photo by L.R. Heckard, printed on a calendar featuring rare and endangered plants in the early 1980s.

Figure 63. *Castilleja uliginosa*, Botany Greenhouses, University of California, Berkeley. Plant grown from tissue clone, photographed 21 June 1985. Although presumed extirpated in the wild, the species continues to be grown and maintained at UC Berkeley Botanical Garden. Photo by Egger.