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CASTILLEJA AMBIGUA VAR. *HECKARDII* (OROBANCHACEAE): A NEW VARIETY FROM SAN LUIS OBISPO COUNTY, CALIFORNIA

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ABSTRACT

Castilleja ambigua var. **heckardii** Egger & Excoffier, **var. nov.**, is described from San Luis Obispo Co., California. It is included within *Castilleja ambigua* based on strong similarities in growth form and vegetative morphology and in some characters of the inflorescence. It is distinguished from the other named varieties of *C. ambigua* primarily by the coloration of the corolla and of the bract tips, as well as by its disjunct range. The new variety occurs on grassy bluffs and ridge tops along the coastal terrace of northwestern San Luis Obispo Co., California. It is a rare and localized endemic and its conservation status needs prompt evaluation.

While *Castilleja ambigua* Hook. & Arn. as a species is a well-known element of the coastal flora of the western United States since its description in 1833, its range was thought for many years to extend only from the Monterey Bay region of northern Monterey Co., California, northward to coastal southwestern Vancouver Island, British Columbia (Jepson 1925; Keck 1927, 1951; Munz & Keck 1968). However, starting with a collection by I.J. Condit in 1912 (UC), a small number of collections from the coastal bluffs and terraces of northwestern San Luis Obispo Co., California began to accumulate in the collections at UC/JEPS and OBI. These early collections were without exception initially identified as the synonymous *Orthocarpus castillejoides* Benth., without infraspecific designation. Most were subsequently annotated to either *Castilleja ambigua* subsp. *ambigua* or *C. ambigua* subsp. *insalutata* (Jeps.) Chuang & Heckard. The first published references to the presence of *C. ambigua* in San Luis Obispo County appear to be those of Hoover (1970) and later of Chuang and Heckard (1991). In the recent Vol. 17 of the Flora of North America (Egger et al. 2019) four varieties were recognized within *C. ambigua*, but the San Luis Obispo County collections were erroneously dismissed as referrable to other species or to possible hybridization, due to the anomalous appearance of the plants in the low-resolution images available at the time of examination.

By 2020, Excoffier and others posted close-up, higher quality field photographs from a population of the San Luis Obispo plants to the iNaturalist website, and these, as well as some additional observations posted on other portals by other botanists from the county, were subsequently reviewed by Egger. Comparing these field photos with the improved specimen images posted on the Consortium of California Herbaria web portal quickly led to the realization that all the known populations of *Castilleja ambigua* in San Luis Obispo County are uniformly divergent morphologically and geographically disjunct from the known forms of the species, and they are described here as a novel entity.

CASTILLEJA AMBIGUA var. **HECKARDII** J.M. Egger & Excoffier, **var. nov. TYPE: USA. California.** San Luis Obispo Co.: Ca. ½ mi S of Piedras Blancas lighthouse, grassy bluffs above ocean, 14 May 1979, *L.R. Heckard 5007* with R. Bacigalupi (holotype: JEPS). Figures 1-12.

Similar to the previously described forms of *Castilleja ambigua* Hook. & Arn. in growth form and vegetative characters but differing from them in coloration and markings of the corolla as well as in phenological patterns of color change in the corollas and in bract and calyx lobe apices, disjunct distribution, and somewhat divergent habitat preference.

Plants annual, 6–25 cm tall, with thin, branched, and fibrous roots. **Stems** 1–ca. 10, unbranched or more commonly with several decumbent-ascending branches from near the base and often branching again, usually from +/- midstem with ascending side-branches, dull straw-brown to dull reddish-purple, sparsely to densely pilosulous with a mix of fine, stipitate-glandular hairs and smaller numbers of non-glandular hairs. **Leaves** 0.5–2.8 cm long, narrowly to broadly lanceolate, oblanceolate or ovate, entire or with 1 (–2) pairs of linear to lanceolate lobes, 2–10 mm long, apices acute to rounded; sparsely to moderately pilosulous and usually stipitate-glandular, as with the stems; pale green to brownish or dull reddish-purple. **Inflorescences** 1.5–8.0 cm long, with few to many, densely ranked, sessile to short-pedicellate flowers. **Bracts** ovate to broadly lanceolate, 5–22 mm long, divided into 3–5 divaricate-ascending lobes or rarely entire, the central lobe broader and lanceolate to linear-lanceolate with acute to obtuse or rounded apices, the lateral lobes narrower and linear to linear-lanceolate, the apices mostly acute; moderate to densely pilosulous and usually stipulate-glandular; brownish, dull reddish-purple or sometimes pale greenish proximally, with distal tips usually white at first but rapidly becoming pink to pink-purplish with age, sometimes pink-purplish throughout development. **Calyces** 15–20 mm long, divided subequally into four linear lobes, each 8–10 mm long, pilosulous to hispidulous and often stipitate-glandular, pale greenish proximally, becoming purplish-brown distally, often with white to pink or pink-purple apices, aging as in bracts. **Corollas** 15–30 mm long, with the beak, lower lip, and often a distal portion of the tube conspicuously exserted from calyces at full anthesis; tubes 11–25 mm long, white and glabrescent proximally, becoming +/- pilosulous and pale pink-purple distally especially on the adaxial surface; lower lip 4–7 mm long, with three divergent, saccate pouches 2–4 mm wide, pilosulous, white proximally, with an abrupt transition to purple on the distal 1/3–2/3, and each with a purplish distal tooth ca. 1.0 mm long and a dark spot near its attachment to the pouch; beaks 5–9 mm long, slightly curved in the abaxial direction, densely glandular-puberulent, purplish throughout; entire corolla often becoming pink-purple with age. **Stigmas** well-exserted, capitate to slightly expanded distally or sometimes obscurely bi-lobed. **Anthers** ca. 1.0 mm long, inconspicuously exserted at full anthesis. **Capsules** 8–12 mm long, ovoid with a slightly curved, acuminate tip, glabrous, stramineous. **Seeds** numerous, ca. 0.8 mm long, short-ovoid, brownish; coat tight-fitting, reticulate, cells mostly polygonal-ovate, radial walls fairly shallow and smooth or obscurely striate, inner tangential walls membranous and apparently unruptured at maturity. **Chromosome number**: $n = 12$, based on two counts from different subpopulations near the type locality by T.I. and F.M. Chuang (Chuang & Heckard 1982).

Paratypes. USA. California. San Luis Obispo Co.: San Carpoforo, Jun 1912, *Condit s.n.* (UC); Piedras Blancas, 15 Jun 1938, *Eastwood & Howell 5986* (JEPS); just S of mouth of Arroyo de la Cruz, in moist places on hilltop, 35.70715, -121.306318, 30 May 1950, *Hoover 7947* (JEPS, OBI); N of Piedras Blancas Point, ($n = 12$ from plant of this population), 20 May 1978, *Chuang 7694* (JEPS); S of Piedras Blancas Point, open, grassy flat near coastal bluff ($n = 12$ from plant of this population), 20 May 1978, *Chuang 7696* (JEPS); along ridge system between Arroyo de la Cruz and Arroyo del Oso, 5-180 m elevation, 14 May 1983, *Keil 16994* (OBI); near top of grassy ridge on coastal terrace, NNE of Calif Hwy 1 and S of Arroyo de la Cruz, 35.70126, -121290639, 21 Jun 2020, *Excoffier s.n.* (CAS, RSA, US, WTU).

Additional images examined. San Luis Obispo Co.: Ridge just S of Arroyo de la Cruz, E of Hwy 1, 20 Jun 2012, *Winchell* (https://calphotos.berkeley.edu/cgi/img_query?seq_num=414926&one=T); on coastal bluff S of Piedras Blancas lighthouse, N of elephant seal viewing areas, 13 Jun 2005, *Hacker* (https://calphotos.berkeley.edu/cgi/img_query?seq_num=183569&one=T) [photo is of a plant with a fascicular stem, see Fig. 12]; Lat: 35.702603, Lon: -121.292289, 20 Jul 2019, *Excoffier* (https://www.inaturalist.org/observations/29219460) [latest date of documented flowering]; Lat: 35.70126, Lon:-121.290639, 13 Jun 2020, *Excoffier* (https://www.inaturalist.org/observations/49643112**)**; Lat: 35.703571 Lon: -121.295681, 21 Jun 2020, *Stickrod* (https://www.inaturalist.org/observations/50741307) [see Figs. 7-8].

Etymology. The new variety is named in memory of Lawrence R. Heckard (1923-1991), Curator of The Jepson Herbarium and Library at the University of California, Berkeley (1968-1991). In addition to his diverse contributions to botany in general, Heckard was a dedicated specialist on *Castilleja* and related genera. Along with his frequent collaborator, T.I. Chuang, Heckard published numerous seminal papers concerning the taxonomy and relationships of the Castillejinae genera. In addition, Heckard graciously corresponded with Egger and actively encouraged his nascent studies of the Castillejinae from 1985 through 1991. Moreover, Heckard promoted the study and conservation of the flora of California on many levels and to many audiences, and he was a mentor and inspiration to a wide variety of aspiring botanists. It is a privilege to name this variety in his honor.

Recommended common name. Heckard's Owl's-clover.

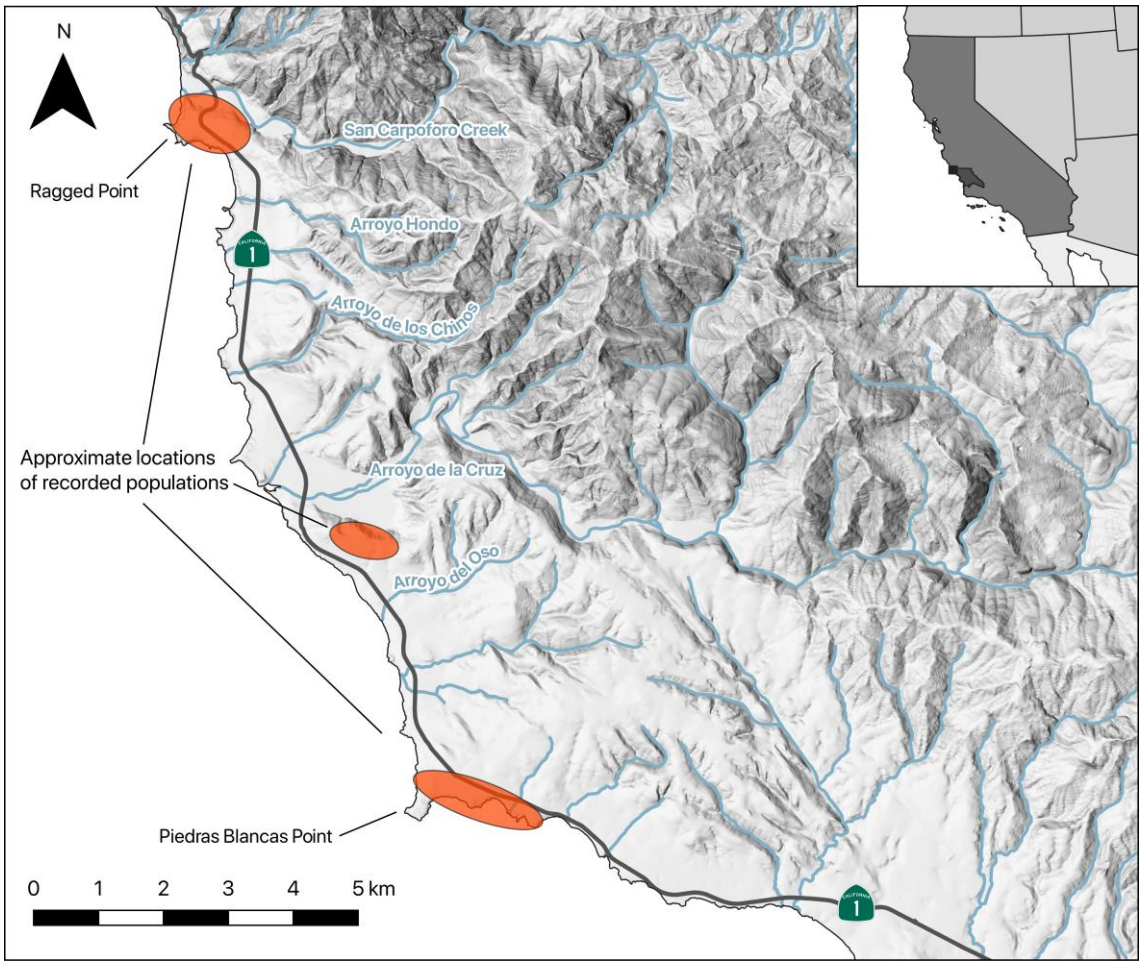

Figure 1. Approximate locations of documented populations of *Castilleja ambigua* var. *heckardii*.

Figure 2. Holotype collection of *Castilleja ambigua* var. *heckardii*, *Heckard 5007*, JEPS.

Figure 3. *Castilleja ambigua* var. *heckardii*, *Condit s.n.*, UC. Paratype and earliest known collection.

Figure 4. *Castilleja ambigua* var. *heckardii*, *Hoover 7947*, OBI. Paratype.

Figure 5. *Castilleja ambigua* var. *heckardii*, *Chuang 7696* (JEPS). Paratype. Chromosome count of *n* = 12.

Phenology, ecology, and associated species. *Castilleja ambigua* var. *heckardii* is known to flower from early to mid-May to at least mid-July. It occurs in shallow depressions that may be vernally moist in sandy soils on coastal bluffs and ridge tops in dryish coastal terrace grasslands with a mix of native species and invasive grasses. Unlike some other forms of *C. ambigua*, it is not known to occur in salt marshes or in sand dune communities. The elevations of the known populations range between 50-180 meters. Associated species include *Bloomeria humilis*, *Calochortus luteus*, *Brodiaea terrestris*, *Armeria maritima* subsp. *californica*, *Ceanothus maritimus*, *Eryngium armata*, *Linum bienne*, *Lupinus* sp., *Plantago lanceolata*, *Triphysaria pusilla*, *Grindelia* sp., *Carex obispoensis*, *Juncus occidentalis*, *Stipa pulchra*, *Aira caryophyllea*, *Briza maxima*, and other invasive grasses. While other *Castilleja* species, including *C. affinis* var. *affinis*, occur in adjacent habitats, none occurs intermixed with plants of *C. ambigua* var. *heckardii*, and no evidence of any kind of hybridization or genetic introgression with other species has been observed.

Distribution and range. All known populations of var. *heckardii* occur on the coastal bluffs and terraces of a small portion of northwestern San Luis Obispo County, from about one kilometer southeast of Piedras Blancas Point northwestward to the vicinity of Ragged Point and the mouth of San Carpoforo Creek (Fig. 1). All known populations are within a kilometer of the immediate coast of the Pacific Ocean. Additional populations may well occur in the region, especially to the southeast, on the western margins of the Hearst Ranch, though access to this area is restricted.

The limited range of *Castilleja ambigua* var. *heckardii* is disjunct from that of all other varieties of the species by at least 100 km, apparently isolated by the sheer cliffs and rough topography of the Santa Lucia Mountains in the Big Sur region. All known and verified herbarium specimens and photo-documented occurrences of *C. ambigua* in San Luis Obispo County are of the new variety.

Conservation status. *Castilleja ambigua* var. *heckardii* appears to have a very limited range and a patchy distribution within that small range. Plants are known from three clusters along a straight-line distance of 12-14 km, including San Carpoforo Creek/Ragged Point, Arroyo de la Cruz (erroneously labeled as Arroyo de la Laguna on some maps), and near Piedras Blancas Point. The only existing population estimate for any of these populations was made by Excoffier in 2020, with the Arroyo de la Cruz population estimated to be approximately 1000 plants. He was not able to locate any plants in the region around Piedras Blancas Point. The San Carpoforo Creek population, the first collection site of var. *heckardii*, remains undocumented since the original collection in 1912, and that population may be very small or even have been extirpated in the last century. Appropriate habitat may also be more limited in that area. With these considerations, we recommend immediate evaluation of this variety for listing under both the federal Endangered Species Act and by the State of California. We also recommend that the California Native Plant Society designate *C. ambigua* var. *heckardii* with a California Rare Plant Rank of 1B.1, Rare and Endangered in California and Elsewhere. Under IUCN (2000) Red List criteria, var. *heckardii* qualifies as Endangered (EN) – High risk of extinction in the wild, based on extent of occurrence estimated to be less than about 100 km^2. In addition to low population numbers and very small range, var. *heckardii* is vulnerable to threats from the rapid proliferation of overtopping exotic grasses and other invasive weedy species in its habitat, as well as from excessive livestock grazing. Studies are needed to establish a management plan that minimizes both threats.

Relationships and identification. *Castilleja ambigua* is a complex and polymorphic species endemic to the west coast region of North America, from northwestern San Luis Obispo County, California north to extreme southwestern British Columbia, Canada. It was originally placed in the formerly paraphyletic genus *Orthocarpus* Nutt. as *O. castillejoides* Benth. Jepson (1925) described *O. castillejoides* var. *insalutatus* Jeps., and Keck, in his revision of *Orthocarpus* (1927) added another infraspecific segregate, *O. castillejoides* var. *humboldtiensis* Keck. In later publications, Keck (1951)

and Munz (1959) reduced var. *insalutatus* to synonymy under the typical variety. Later, *O. castillejoides* and the other species of the former *Orthocarpus* sect. *Castillejoides* A. Gray and sect. *Cordylanthoides* Keck were moved into *Castilleja* in Chuang and Heckard's landmark revision of the Castillejinae (1991). At that time, Chuang and Heckard adopted the earlier-published name, *C. ambigua* Hook. & Arn. for *O. castillejoides* and changed the rank of the infraspecific groupings from variety to subspecies. They also resurrected Jepson's var. *insalutatus* as subsp. *insalutata* Chuang & Heckard. This nomenclature was adopted in The Jepson Manual (Chuang & Heckard 1993). Subsequently, Egger (2008, 2019) reestablished the use of varieties for the infraspecific entities within *C. ambigua*, as part of a broader attempt to provide a standardized infraspecific nomenclature for the entire genus. Finally, Egger et al. (2012) described a fourth entity, *C. ambigua* var. *meadii* Egger & Ruygt from Napa Co., California. However, recent molecular work indicates that var. *meadii* is in a clade separate from the other varieties of *C. ambigua* (Jacobs et al. 2018) and that it is likely deserving of species rank, though this status change is not yet formally published. Field photos of all four previously accepted varieties of *C. ambigua* are presented in Figure 6.

Castilleja ambigua var. *humboldtiensis* (Keck) Egger and *C. ambigua* var. *insalutata* (Jeps.) Egger are both strictly coastal, occurring in the margins of estuarine salt marshes or on sandy coastal meadows and bluffs. The typical variety of *C. ambigua* is more adaptable and far more widespread, occurring in a number of complex and variable forms both along the coast and somewhat sporadically in grasslands and meadow situations some miles in from the immediate coast. *Castilleja ambigua* var. *meadii* is ecologically unique in its preference for the margins of wet meadows over basaltic substrates, and it is limited to a few sites in a small portion of south-central Napa County. *Castilleja ambigua* var. *heckardii* is somewhat unique in that its occurrence is apparently limited to fairly dry grassland communities, though it does overlap with some populations of var. *ambigua* in this respect.

We place this newly recognized entity at varietal rank within *C. ambigua* because of its close similarity in stature, general vegetative morphology, bract coloration patterning, and near-coastal occurrence. However, var. *heckardii* is immediately separable from the other forms of *C. ambigua* by the strikingly different and strongly consistent coloration of the fresh corollas noted in the key below, as well as by its disjunct range. While these differences could be reasonably used to justify its treatment at the species rank, we prefer for now the more conservative approach of varietal designation, in line with the presently accepted taxonomy of the *C. ambigua* complex, pending the results of ongoing morphological and molecular studies of the entire group.

San Luis Obispo County, and especially the coastal portion thereof, is well known as a center of endemism within California region (Hoover 1970; Keil 2019). *Castilleja densiflora* (Benth.) Chuang & Heckard var. *obispoensis* (Keck) Egger is another annual owl's-clover form largely endemic to the county, including the coastal terrace grasslands, as is the recently described *Pedicularis rigginsiae* Keil (Keil 2019), which occurs not far from the populations of *C. ambigua* var. *heckardii* in dwarf maritime chaparral. Other local endemics include *Ceanothus maritimus*, *Ceanothus hearstiorum*, *Arctostaphylos cruzensis*, *Arctostaphylos hookeri* subsp. *hearstiorum*, and *Bloomeria humilis* (D. Keil, pers. comm., 2021). While *C. densiflora* var. *obispoensis* is reported from the vicinity of the Arroyo de la Cruz population of *C. ambigua* var. *heckardii*, it appears to favor a somewhat different habitat and does not occur at the same sites. There are no reports of var. *obispoensis* near the other two population clusters of var. *heckardii*.

Two published chromosome counts for plants from adjacent subpopulations near the type locality show *Castilleja ambigua* var. *heckardii* to be diploid, with meiotic count of ***n = 12*** (as *Orthocarpus castillejoides*, Chuang & Heckard 1982). These counts are consistent with all other published counts for all four of the previously accepted varieties of *C. ambigua* (Anderson 1965; Atsatt 1966; Chuang & Heckard 1982; Egger et al. 2012). These counts suggest that none of the forms of *C. ambigua* is of allopolyploid hybrid origin.

It should also be noted that in a recently published flora for Napa County (Ruygt 2020), *Castilleja ambigua* var. *meadii* is referred to as, "*Castilleja ambigua* ssp. *meadii* D. Tank, M. Egger, and J. Ruygt." This combination is both invalidly published and incorrectly attributes the authorship of the taxon, which was validly published as var. *meadii* Egger & Ruygt (Egger et al. 2012).

Key to the varieties of *Castilleja ambigua*

1. Bract lobes linear; stems erect; moist inland meadows and vernal pools on volcanic substrates; south-central Napa Co., California ..... var. **meadii**
1. Bract lobes linear to lanceolate or oblong; stems +/- decumbent, at least proximally; margins of coastal salt marshes and brackish estuaries, coastal sandy bluffs and meadows, mesic to somewhat xeric near-coastal grasslands; British Columbia to San Luis Obispo Co., California.

2. Bracts always pink-purple to purple distally; stems unbranched or few-branched from mid stem; salt marshes; Humboldt Bay region, nw California ..... var. **humboldtiensis**
2. Bracts white distally, at least at first, rarely pink or cream; stems often branched from base; salt marshes, sandy coastal bluffs and meadows, near-coastal grasslands**;** British Columbia to San Luis Obispo Co., California.

3. Corolla beaks usually white or yellow, abaxial lip pouches yellow; salt marshes, sandy coastal bluffs, inland grasslands; s British Columbia to c California ..... var. **ambigua**
3. Corolla beaks usually pink to purplish, abaxial lip pouches yellow, becoming white and then reddish to soft pink-purple with age; or white proximally and purple distally; grassy coastal bluffs and ridges or coastal meadows.

4. Abaxial lip pouches of corollas yellow, often becoming white and then reddish to soft pink-purple with age; sandy coastal meadows and bluffs in the vicinity of Monterey Bay, and w San Francisco Bay, California ..... var. **insalutata**
4. Abaxial lip pouches of corollas white proximally and abruptly purple distally, never yellow, coastal bluffs and ridges of nw San Luis Obispo Co., California ..... var. **heckardii**

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Figure 6. Previously described varieties of *Castilleja ambigua*. Upper left: var. *ambigua*; right: var. *meadii*; lower left: var. *humboldtiensis*; right: var. *insalutata*. All photos by J.M. Egger.

Figure 7. *Castilleja ambigua* var. *heckardii*. Photo by M. Stickrod, south of Arroyo de la Cruz, 21 June 2020.

Figure 8. *Castilleja ambigua* var. *heckardii*. Photo by M. Stickrod, S of Arroyo de la Cruz, 21 June 2020.

Figure 9. *Castilleja ambigua* var. *heckardii*. Photo by P. Excoffier, S of Arroyo de la Cruz, 21 June 2020.

Figure 10. *Castilleja ambigua* var. *heckardii*. Photo by P. Excoffier, S of Arroyo de la Cruz, 21 June 2020.

Figure 11. *Castilleja ambigua* var. *heckardii* in habitat with associated plant species. Photo by P. Excoffier, S of Arroyo de la Cruz, 21 June 2020.

Figure 12. *Castilleja ambigua* var. *heckardii*, unusual specimen apparently exhibiting stem fasciation, recorded in a significant number of both annual and perennial *Castilleja* species (Egger, unpubl. data). Photo by D. Hacker from the vicinity of the type locality, south of Piedras Blancas Point, 13 June 2005.