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ELEVATION TO SPECIES RANK OF TWO RANGE-RESTRICTED VARIETIES OF *CASTILLEJA AMBIGUA* (OROBANCHACEAE) FROM CALIFORNIA

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ABSTRACT

Castilleja ambigua var. *meadii*, a narrow endemic of Napa Co., California, and *Castilleja ambigua* var. *heckardii* of San Luis Obispo Co., California, are each elevated to the rank of species as **Castilleja meadii** Egger & Ruygt (Egger & Ruygt), **comb. et stat. nov.** and **Castilleja heckardii** (Egger & Excoffier) Egger & Excoffier, **comb. et stat. nov.**

In recent years, the authors have described two morphologically and ecologically distinctive and highly range restricted forms of *Castilleja* as new varieties of *Castilleja ambigua* (Hook. & Arn.) Chuang & Heckard (Egger et al. 2012; Egger & Excoffier 2021). *Castilleja ambigua* var. *meadii* was included in the Flora of North America *Castilleja* treatment (Egger et al. 2017), but *C. ambigua* var. *heckardii* was not yet described at that time. Further field studies of both taxa and accumulation of recent molecular and ecological evidence have led us to conclude that each former variety is better treated at the rank of species, and each is proposed as such below.

In both cases, an equivalent goal is toward a more consistent species concept in *Castilleja*, especially regarding the many geographically disjunct, ecologically and/or geographically restricted, and morphologically distinctive taxa. Such species are presently isolated reproductively from their presumed ancestral species and are on unique evolutionary paths. These species stand in contrast to many other *Castilleja* taxa that represent widespread species with genetic and morphological complexities and that are potentially ongoing interacting systems of morphological varieties and forms (e.g., *Castilleja affinis* Hook. & Arn., *Castilleja integrifolia* L.f., *Castilleja miniata* Douglas ex. Hook., *Castilleja pallida* (L.) Spreng., *Castilleja pilosa* (S. Wats.) Rydb., *Castilleja subinclusa* Greene). In this latter group, we tentatively include the three remaining varieties of *C. ambigua*, which are largely restricted to coastal and near coastal estuarine marshes and nearby dunes and sandy bluffs, and these forms also deserve careful and detailed analysis in future studies.

Castilleja meadii (J.M. Egger & J.A. Ruygt) J.M. Egger & J.A. Ruygt, **comb. et stat. nov.**
Castilleja ambigua var. *meadii* J.M. Egger & J.A. Ruygt, Phytoneuron 2012-68: 2, 2012. *Castilleja ambigua* subsp. *meadii* Tank, Egger, & Ruygt, nom. inval., Fl. Napa County (Ruygt), 274, 2020.

In the process of describing *Castilleja ambigua* var. *meadii*, Egger and Ruygt discussed which taxonomic rank was most appropriate, but they hesitantly chose varietal status within *C. ambigua* because of the close similarity of the characters of the corolla to that of typical *C. ambigua*. However, *Castilleja meadii* is easily separable from all forms of *C. ambigua* by its upright growth form and distinctive leaf morphology. It is also distinguished by its specialized habitat in vernally wet, shallow, igneous-derived clay soils. *Castilleja meadii* occurs well inland from the coast, in a small cluster of subpopulations in south-central Napa Co., California (Egger et al. 2012). Subsequently, in a study of clay soil endemism in the California flora, the *meadii* form was the sole representative of the Orobanchaceae identified as exhibiting such characteristics and was ranked as a "strict endemic" to clay soils (Fryer et al. 2025). In addition, recent molecular work has shown *C. meadii* to be genetically distinct from the other infraspecific taxa of *C. ambigua* evaluated and likely deserving of recognition at species rank (Jacobs et al. 2013, 2018). The more recently described *C. ambigua* var. *heckardii* was not evaluated in the studies by Jacobs et al.

Castilleja heckardii (J.M. Egger & Excoffier) J.M. Egger & Excoffier, **comb. et stat. nov.** *Castilleja ambigua* var. *heckardii* J.M. Egger & Excoffier, Phytoneuron 2021-15: 2. 2021.

In many ways, the case for *Castilleja heckardii* is very similar to that of *C. meadii*. Both are very rare, localized endemics, disjunct from closely related species, though both are well-separated from each other in morphology, habitat preference, and phenology. A key and field photographs useful for separating *C. heckardii* from *C. meadii*, as well as from all other forms of *C. ambigua*, are provided in Egger and Excoffier (2021). *Castilleja heckardii* occurs in a very small area in the far northwest corner of San Luis Obispo County in vernally moist depressions that are typically dry by the time the plants begin flowering on high bluffs and coastal terraces, and they are closely associated with and likely parasitic on *Eryngium armatum* (S. Wats.) Coult. & Rose (Egger & Excoffier 2021). While *C. heckardii* was not formally evaluated or ranked as to clay soil affinity by Fryer et al. (2025), due to the lack of voucher specimens with notes on soil texture, they included the following note: "We are aware of several taxa with very small ranges suggesting those taxa are restricted to clay soils (e.g., *Castilleja ambigua* var. *heckardii* ... ." This species is also notable and unique among its presumed relatives in the coloration patterns of the corollas, suggesting a switch in pollinator preferences.

Both *Castilleja meadii* and *C. heckardii* are known to be diploids (*n=12*) and so are not likely of hybrid polyploid derivation. While other *Castilleja* species occur in the general vicinity of both *C. meadii* and *C. heckardii*. we have observed no evidence of morphological variation or intermediate characters suggestive of genetic introgression in either species.

Finally, it should be noted that both species addressed in this taxonomic update are presently listed by NatureServe (2025) as "Critically Endangered Varieties," and we recommend both for reclassification as Critically Endangered at species rank.

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