

CASTILLEJA COCCINEA AND C. INDIVISA (OROBANCHACEAE)

GUY L. NESOM

2925 Hartwood Drive
Fort Worth, Texas 76109
www.guynesom.com

J. MARK EGGER

Herbarium, Burke Museum of Natural History and Culture
University of Washington
Seattle, Washington 98195-5325
m.egger@comcast.net

ABSTRACT

Castilleja coccinea and *C. indivisa* are contrasted in morphology and their ranges mapped in detail in the southern USA, where they are natively sympatric in small areas of Oklahoma, Arkansas, and Louisiana. *Castilleja indivisa* has recently been introduced and naturalized in the floras of Alabama and Florida. *Castilleja ludoviciana*, known only by the type collection from southwestern Louisiana, differs from *C. coccinea* in subtire leaves and relatively small flowers and is perhaps a population introgressed by *C. indivisa*.

Castilleja coccinea and *C. indivisa* are allopatric except in small areas of Oklahoma, Arkansas, and Louisiana, but assessments of their native distributions are not consistent among various accounts (e.g. Thomas & Allen 1997; Turner et al. 2003; OVPD 2012; USDA, NRCS 2013). Morphological contrasts between the two species, via keys in floristic treatments (e.g., Smith 1994; Wunderlin & Hansen 2003; Nelson 2009; Weakley 2012), have essentially repeated the differences outlined by Pennell (1935). The current study presents an evaluation and summary of the taxonomy of these two species.

We have examined specimens at CAS, TEX-LL, SMU-BRIT-VDB, MO, NLU, NO, USF, WS, and WTU and viewed digital images available through Florida herbaria and databases.

CASTILLEJA COCCINEA (L.) Spreng., Syst. Veg. 2: 775. 1825. *Bartsia coccinea* L., Sp. Pl. 2: 602. 1753. *Euchroma coccinea* (L.) Nutt., Gen. N. Amer. Pl. 2: 54. 1818. **LECTOTYPE:** (Jarvis 2007): **USA. Virginia.** No other collection data, *J. Clayton 293* (BM digital image!).

Castilleja coccinea forma *alba* Farwell, Amer. Midl. Naturalist 8: 276. 1923. **TYPE: USA. Michigan.** Oakland Co.: Goodison, 6 Jun 1923, *O.A. Farwell 6507* (BLH digital image!).

Castilleja coccinea forma *lutescens* Farwell, Amer. Midl. Naturalist 8: 276. 1923. **TYPE: USA. Michigan.** Oakland Co.: Goodison, 6 Jun 1923, *O.A. Farwell 6506* (BLH digital image!).

Castilleja coccinea forma *pallens* (Michx.) Pennell, Monogr. Acad. Nat. Sci. Philad. 1: 535. 1935. *Bartsia coccinea* var. *pallens* Michx., Fl. Bor.-Amer. 2: 17. 1803. **TYPE:** No type specified in protologue. "Bracteis lutescentibus. Rarior." Pennell cited the authorship of the original name as "Pursh, Fl. Amer. Sept. 429. 1814" and assumed that the name was intended at the rank of forma, but Pursh merely repeated the earlier phrasing of Michaux.

Castilleja ludoviciana Pennell, Monogr. Acad. Nat. Sci. Philad. 1: 540. 1935. **TYPE: USA. Louisiana.** Jeff Davis Par.: Low prairies, Welsh, 17 May 1915, *E.J. Palmer 7656* (holotype: MO! digital image!, Fig. 1; isotypes: CAS!, PH, US!, WS!). Annotated as *Castilleja coccinea* by K.A. Vincent in 1981.

Annual herbs, fibrous-rooted. **Stems** erect, 12–50 cm, usually unbranched, short villous with fine, eglandular hairs and much shorter, glandular hairs. **Leaves**: cauline oblong-lanceolate to narrowly oblong-lanceolate or linear-lanceolate, 2–7 cm, never subclasping, consistently with 1–3 approximately paired, linear to narrowly lanceolate lobes (2–)5–25 mm, rarely entire (e.g., Louisiana, Minnesota); basal in persistent rosette though often withered at anthesis, oblanceolate to oblong-lanceolate, 1–3 cm, unlobed, discontinuous in morphology from the cauline; surfaces of basal and cauline hirsutulous-puberulent. **Inflorescence** spicate, unbranched, 3–35 cm (longest in fruit), proximal internodes 2–4.5 cm in fruit. **Bracts** 14–22 mm, proximal lanceolate with 3 lanceolate lobes, apices acute, all green, distally becoming obovate in outline and shorter, 3-lobed divided ca. 1/2 the bract length, or the middle lobe sometimes with 1–2 short lateral lobes, distally red (rarely yellow), apices acute to obtuse. **Flowers** sessile to subsessile; calyces 17–28 mm, divided 1/3–1/2; corollas 18–25 mm, usually exserted 3–7 mm beyond the calyx apex, galea 8–10 mm, 1/4–1/3 length of the tube, greenish with thin, yellowish margins, teeth 2–4(–5) mm, green to yellowish, apically pink to yellow; stigma exserted. **Seed coat** shallowly foveolate-reticulate.

Flowering Apr–Jun(–Jul). Low meadows and fields, ditch and swamp edges, bogs, prairies, roadsides, beach ridges and dunes, jack pine plains, rocky woodlands, sandstone outcrops, limestone ledges, granite cliffs; 150–3300(–4100) ft; Ala., Ark., Conn., Del., Fla., Ga., Ill., Ind., Iowa, Kans., Ky., La., Maine, Md., Mass., Mich., Minn., Miss., Mo., N.H., N.J., N.Y., N.C., Ohio, Okla., Penn., R.I., S.C., Tenn., Va., Wis., W.Va.; Man., N.S., Ont., Sask.

Yellow-bracted plants (*Castilleja coccinea* forma *lutescens* Farwell), otherwise similar to the species in its regional expression, occur sporadically over the range of the species (e.g., Arkansas–Izard Co.; Illinois–Lake Co.; Indiana–Pulaski Co., Starke Co.; Michigan–Cass Co., Oakland Co.; Minnesota–Morrison Co.; Oklahoma–Cherokee Co., Ottawa Co.).

Occurrences of *Castilleja coccinea* in Louisiana (Fig. 2) are documented by these collections: Calcasieu Par.: Lake Charles, prairies, 2 Apr 1911, *R.S. Cocks s.n.* (NO). Jeff Davis Par.: Welsh, prairies, 28 Mar 1906, *R.S. Cocks s.n.* (NO). Jeff Davis Par.: Welsh, low prairies, 17 May 1915, *E.J. Palmer 7656*, the type of *C. ludoviciana*. Rapides Par.: Alexandria, no date, *J. Hale s.n.* (NO, fide Pennell 1935). In Texas the only bona fide record for *C. coccinea* is from Bowie County, as documented by Singhurst et al. (2011).

Pennell (1935) described *Castilleja ludoviciana* as a species and distinguished it and *C. coccinea* as a pair from *C. indivisa* by the following contrasts (p. 535).

- | | |
|---|-------------------------------------|
| 1. Lower lip of corolla very short, thickened, green; corolla 20–25 mm long; leaf blades entire or slightly lobed; basal rosettes not or scarcely formed, certainly not persisting until anthesis | Castilleja indivisa |
| 1. Lower lip of corolla more developed, distally thin and yellowish; basal leaf rosettes more or less evident. | |
| 2. Corolla 20–25 mm long, the lower lip less than 1/3 length of galea; cauline leaf blades pinnately lobed; basal leaf rosettes well-developed, persisting until after anthesis | Castilleja coccinea |
| 2. Corolla 13–15 mm long, the lower lip about 1/2 length of galea; cauline leaf blades entire or nearly so; basal rosettes less developed, scarcely evident at anthesis | Castilleja ludoviciana |

We confirm the distinction of *Castilleja indivisa* in generally the same features, particularly leaf morphology and arrangement. As noted by Pennell, the lower corolla lip is relatively shorter in *C. indivisa* but the morphology of the lip in *C. coccinea* apparently is more variable than he surmised.



Figure 1. *Castilleja ludoviciana* Pennell, holotype (MO).

The collection described by Pennell as *Castilleja ludoviciana* was made from southwestern Louisiana (Fig. 2), where *C. coccinea* and *C. indivisa* are sympatric in native range, at least historically. The entire-margined cauline leaves of *C. ludoviciana* and the short calyces (14–15 mm) and corollas (13–15 mm), as recorded by Pennell and confirmed here in study of the holotype and isotypes, distinguish it from *C. coccinea*.

Most of the features of *Castilleja ludoviciana* (Fig. 1) are within the range of variation of *C. coccinea* — the cauline leaves are not clasping and the basal leaves of *C. ludoviciana* are the same as those found in many populations of typical *C. coccinea*, where they vary in persistence in an unwithered condition. In *C. ludoviciana* and commonly across the range of *C. coccinea*, the basal leaves are somewhat withered but mostly persistent and still morphologically distinct from the cauline. Lobed-leaf individuals occur commonly as population variants throughout the range of *C. indivisa*, but apart from *C. ludoviciana*, entire-leaved variants apparently do not occur in *C. coccinea*.

The entire leaves of *C. ludoviciana*, suggest that it may be a variant of *C. coccinea* showing genetic influence of *C. indivisa*, especially since *C. ludoviciana* lies within the range of *C. coccinea* in an area where *C. indivisa* also occurs (both species as natives in southwestern Louisiana are rare, perhaps extinct, see comments and specimen citations above and below), and a collection of typical *C. coccinea* was made very near the 'ludoviciana' locality. Possible interspecific hybrids between *C. coccinea* and *C. indivisa* might also be sought in eastern Oklahoma and northwestern Arkansas, where the two also are sympatric.

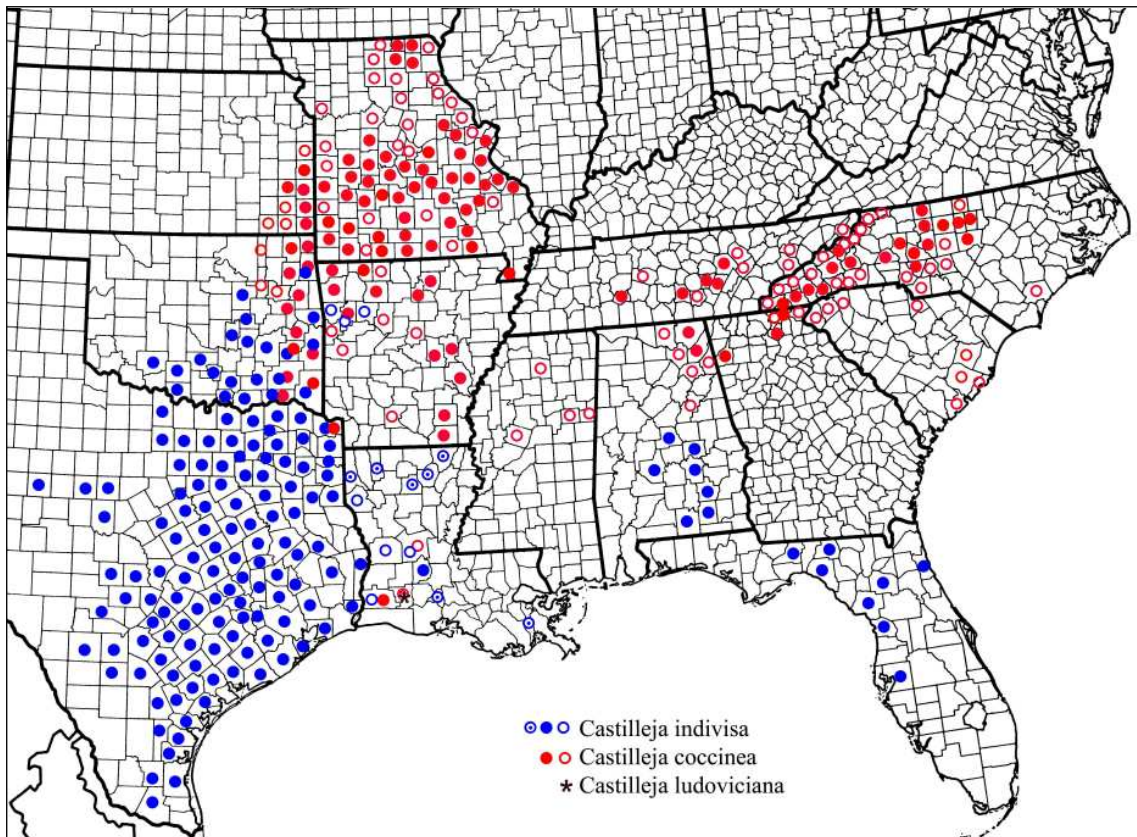


Figure 2. Distribution of *Castilleja coccinea* and *C. indivisa* in south-central and southeastern states of the USA. The distribution of *C. coccinea* continues northward into Canada. Solid symbols are from collections examined; open symbols are from literature and internet sources; dotted symbols (Louisiana) are collections examined from cultivation or immediate garden escapes or from along roadsides where probably seeded for cultivation.

In the present study, *Castilleja coccinea* and *C. indivisa* are distinguished by the following contrasts.

1. Cauline leaves never subclasping, consistently 1–3-lobed, rarely entire (*C. ludoviciana*), basal in a persistent rosette though often withered at anthesis, oblanceolate to oblong-lanceolate, unlobed, discontinuous in morphology from the cauline **Castilleja coccinea**
1. Cauline leaves often subclasping, entire or less commonly 1–2(–3)-lobed (variants scattered through range of the species), basal/lower cauline not forming a distinct rosette but sometimes relatively dense on short internodes, similar in morphology to more distal cauline **Castilleja indivisa**

CASTILLEJA INDIVISA Engelm., Boston J. Nat. Hist. 5: 255. 1845. **TYPE: USA. Texas.** Prairies from Houston to the Colorado, 1844, *F. Lindheimer 284* (holotype: MO 88172! digital image!; isotypes: CGE!, E!, GH!, K-BENTH, K-HOOK!, MO 88171! and 88186! digital images!, PH!, US!).

Castilleja indivisa forma *vivida* Cory, Field & Lab. 17: 65. 1949. **TYPE: USA. Texas.** Refugio Co.: 9 3/4 mi SW of Woodsboro, sandy bank of roadside cut, 28 Mar 1948, *V.L. Cory 54158* (holotype: SMU!).

Annual herbs, fibrous-rooted to nearly taprooted. **Stems** erect, 1(–3) from the base, usually unbranched or with 1–3 branches from the proximal half, (5–)10–45 cm, short villous with fine, eglandular hairs and much shorter, glandular hairs. **Leaves** narrowly lanceolate to linear-lanceolate, 2–8(–9) cm, not forming a distinct basal rosette, sometimes relatively dense proximally on short internodes but similar in size and shape to more distal cauline, sessile, often subclasping, entire or less commonly with 1–2(–3) approximately paired, linear to filiform lobes 1–20 mm, surfaces hirsutulous-puberulent. **Inflorescence** spicate, unbranched, 2–16(–20) cm, villous with fine, eglandular hairs. **Bracts** 5–25 mm, proximal lanceolate-acuminate with acute apices, all green, distally abruptly becoming shorter and obovate to broadly obovate or obtrullate and with rounded to obtuse apices, distal 2/3 scarlet to crimson or salmon pink (rarely white to yellowish), unlobed. **Flowers** sessile to subsessile; calyces 16–22 mm, divided 1/4–1/3 length, primary lobes 6–9 mm, distally red to pink (rarely white to yellowish); corollas (15–)17–24 mm, equal to calyx or exerted 1–6 mm beyond the calyx apex, galea 4–9 mm, ca. 1/5 length of the tube, dorsally yellow to pink, glandular-puberulent, teeth of lower lip 0.5–2 mm, green, thickened, white to yellowish; stigmas exerted, capitate. **Seed coat** shallowly foveolate-reticulate.

Flowering (Mar–)Apr–May(–Jul). Grasslands, blackland prairie, limestone rocky slopes and glades, shell ridges, sandhills, dunes, pastures, old fields, roadsides and ditches, sand and sandy loam, red clay, juniper, oak-juniper, pine, post oak, mesquite-hackberry woodlands; 20–1200 ft; Ala., Ark., Fla., La., Okla., Tex.; Mexico (Aguascalientes, Chihuahua).

As in *Castilleja coccinea*, yellow-bracted individuals of *C. indivisa*, apparently within otherwise red-bracted populations, are scattered over its range (e.g., Brazos, Red River, Travis, Victoria, Wharton counties, Texas). Lobed-leaf variants at least in some cases may reflect introgression from the *C. purpurea* complex (Nesom & Egger 2014).

An enclave of uniformly white-bracted populations occurs in a small area of Nueces Co., Texas, between Aransas Pass and Port Aransas. **Vouchers:** N side of TX 361 on Stedman Island, 1.3 mi ESE of RR crossing on E edge of city of Aransas Pass, common in dredged, probably saline sand, silt and roadbase, grassy roadside, floral parts white in all plants, 4 Mar 1992, *Carr 11714* (TEX); sandy flats on Stedman Island ca. 1 mi ESE of Aransas Pass, 11 Mar 1977, *Duncan 30402* (VDB); along causeway between Aransas Pass and Port Aransas, local populations all white-flowered, scattered, 18 Mar 1996, *Fryxell 5062* (TEX); shell and sand reef between Aransas Pass and Port Aransas, 21 Apr 1935, *Goldsmith s.n.* (PH fide Pennell 1935, TEX); S side of FM 361 at E end of bridge over Redfish Bay enroute to Port Aransas from Aransas Pass, 19 Apr 1988, *Jones 1116* (TAES). A case might be made for the formal taxonomic recognition of this population system.

The northernmost record of *Castilleja indivisa* apparently is a collection for which locality data are minimal: **Oklahoma**. Meadow near Kansas, 2 May 1925, *Small & Wherry 12228* (TEX). A collection of *C. coccinea* was made at the same locality and date: *Small & Wherry 12239* (TEX). Original identifications of both species were correct. Presumably the collections were made from one of the northeastern counties bordering Kansas (Washington, Nowata, Craig, Ottawa), where *C. coccinea* is known from other collections, but the *C. indivisa* record is not mapped in Figure 2.

The only Louisiana collection encountered in this study of *Castilleja indivisa* that apparently occurred in a natural habitat is this: Evangeline Par.: deciduous woods in Chico State Park, ca. 4 mi N of Ville Platte, 3 Apr 1981, *Givens 1961* (NLU). All other collections from Louisiana (Fig. 2) are from explicitly cultivated plants, plants clearly immediately escaped from garden cultivation, or plants recently collected along roadsides of major highways where they probably were seeded as part of wildflower mixes. All Louisiana collections of *C. indivisa* seen in this study were made from 1978 to 1988.

Castilleja indivisa has recently been introduced and is becoming abundant in parts of Alabama and Florida (Fig. 2), disjunct eastward from its main range. Alabama collections all have been from roadsides; the earliest was made in 1995. Florida collections are from roadsides and roadside ditches; the earliest were made in Taylor Co. (1961) and Levy Co. (1991). A 1998 collection from Madison Co., Florida, specifically notes that there were "Large planted colonies on the N side of the interstate and in the median."

Two collections from Mexico are identified here as *Castilleja indivisa*, apparently representing instances of long disjunction, presumably through seeds carried either by wind or by vehicles. **Aguascalientes**. Mpio. San José de Gracia, 12 km SW of La Congoja, ladera riolitica con veg. de bosque abierto de *Quercus*, *Pinus*, y *Juniperus*, 2700 m, 16-17 Oct 1973, *Rzedowski & McVaugh 746* (MICH). **Chihuahua**. SW of Colonia Juárez, near Nuevo Casas Grandes, dry slopes in scrub area, 3 Aug 1965, *Melchert 351* (IA).

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