

STEM FASCIATION IN THE GENUS *CASTILLEJA* (OROBANCHACEAE)

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ABSTRACT

Stem fasciation is documented in 3 annual and 11 perennial species of *Castilleja* through vouchered herbarium collections and field photographs. This abnormality occurs rarely and in species from taxonomically diverse parts of the genus. The common characteristics of fasciation in *Castilleja* are described.

Stem fasciation and the resultant accumulation of unusually massive inflorescences with densely packed flowers has been the subject of considerable interest in the botanical literature, an extensive bibliography of which is provided by Iliev and Kitin (2011). Many papers explore the biology and causes of fasciation (e.g., White 1945, 1948), while others have addressed its occurrence in a wide variety of plant groups (e.g., Hus 1906; Ansari & Daehler 2011; Sinjushin 2016). There is even a Flickr photo group dedicated to photographs of various types of fasciation in plants (Anon. 2021). While White (1945) indicated fasciation has been recorded in unspecified species of Orobanchaceae and Scrophulariaceae (sensu lato), few references to genera or species exhibiting fasciation are available for these families, aside from Ansari and Daehler (2011) for *Verbascum*. The anonymous internet blog, Tentative Plant Scientist (2021) documents stem fasciation in cultivars of the Plantaginaceae genera, *Veronicastrum* and *Digitalis*, as well as in other plant families. I could only find two references to fasciation in the botanical literature involving the genus *Castilleja*, both concerning the type collection of *Castilleja blumeri* Standl., now regarded as a synonym of *C. patriotica* Fernald (Standley 1909; Holmgren 1976). Standley mentioned Blumer's field observations of a fasciated plant that later became part of the isotype sheet at NY (see Fig. 14), then went on to observe that "Fasciation seems to be not at all uncommon in the *Castillejas*; the writer [Standley] noticed several examples of this last summer in specimens of *C. confusa* [= *C. miniata*], found in New Mexico in the Pecos River National Forest." Recently, a photograph of a fasciated plant was included in the paper describing *Castilleja ambigua* Hook. & Arn. var. *heckardii* Egger & Excoffier (Egger & Excoffier 2021). Photos of the specimens referenced in these papers are included here.

While there is consensus in the literature that stem fasciation is the result of mutations in the regulation of early meristem development, the source or sources of such mutations is still under study and may vary from case to case (Iliev & Kitin 2011; Tentative Plant Scientist 2021). Causes proposed in various plant groups outside cultivation include recessive genes, a variety of environmental factors, and physical damage to the plant tissue by invertebrates or through bacterial, viral, or fungal infections. I could find no proposed causes of meristematic cell mutations specific to *Castilleja*.

In my studies of *Castilleja* in the field and the herbarium, I've encountered numerous examples of both fasciated stems and the resultant deformations of the typical inflorescence morphology of the species involved. To document and illustrate these occurrences, I've prepared below an alphabetically arranged gallery of species, composed of images of herbarium specimens and field photographs by myself or by photographers posting on sites such as Flickr and iNaturalist from whom I've obtained permission to present their images. Photos without attribution are my own. In several cases, the fasciated plants were photographed in the field and then collected as specimen vouchers, and images of both are presented in those cases.

The morphological manifestations of stem fasciation in *Castilleja* usually involve a thickening and horizontal compression of the stems, with vertical striations often visible on the stem surfaces, though sometimes obscured by the stem pubescence, and by an often visually striking widening of the inflorescence, with the individual flowers becoming both far more numerous and often more densely ranked than is typical for the species involved. In some cases, there is also a minor lateral compression of the inflorescence, typical of many cases of fasciation in a wide range of plant families, though this is not always the case in *Castilleja*. In species having multiple stems from near the base of the plant, usually only a single stem is fasciated, and fasciated stems sometimes bear unfasciated lateral branches.

Evidence of stem fasciation is documented here for the following naturally occurring *Castilleja* species, including 3 annuals and 11 perennials. These species come from diverse parts of the genus and additional species almost certainly express this developmental abnormality on occasion. However, in only two species, *C. indivisa* and *C. purpurea*, have I encountered more than one example per species, suggesting that this trait is of widespread but rare occurrence among the species of this genus.

Castilleja ambigua var. *heckardii* Egger & Excoffier, Figure 1.

Castilleja arvensis Schltl. & Cham., Figure 2.

Castilleja chromosa A. Nels., Figure 3.

Castilleja chrymactis Pennell, Figures 4.

Castilleja cusickii Greenm., Figures 5-6.

Castilleja foliolosa Hook. & Arn., Figure 7.

Castilleja hispida Benth. var. *hispida*, Figure 8.

Castilleja indivisa Engelm. & A. Gray, Figures 9-10.

Castilleja linariifolia Benth., Figures 11-13.

Castilleja miniata Douglas ex Hook., Figure 14.

Castilleja patriotica Fernald, Figures 15-17.

Castilleja purpurea (Nutt.) G. Don, Figures 18-22.

Castilleja stenophylla M.E. Jones, Figures 23-24.

Castilleja wootonii Standl., Figures 25-26.



Figure 1. *Castilleja ambigua* var. *heckardii*, specimen exhibiting fasciated inflorescence. A typical stem is in the upper right. South of Piedras Blancas Point, San Luis Obispo Co., California, 13 Jun 2005. Photo by Dave Hacker, used with permission.



Figure 2. A fasciated stem of *Castilleja arvensis* in center, with two typical stems on the left. Note also the unfasciated side branch from the fasciated stem. Along the road to Rancho Las Cañadas, N of Huatusco, Veracruz, Mexico, 31 Dec 2020. Photograph by Bodo Nuñez O., used with permission.



Figure 3. Stem fasciation in central stem of fruiting *Castilleja chromosa* also bearing unfasciated branches, Wilcox 21, ASC.



Figure 4. Stem fasciation in *Castilleja chrymactis*, seen in the plant on the left, with two typical stems to the right. Recently deglaciated valley, NE end of Harlequin Lake, near foot of Yakutat Glacier, Russel Fiords Wilderness Area, Alaska, 16 Jul 1998.



Figure 5. Fasciated stem of *Castilleja cusickii*, on left, with typical stem on right. This species is rarely branched except near the base. Along US Hwy 89, 1.0 mi NE of bridge over Ovid Cr., northern Bear Valley, Caribou Co., Idaho, 22 Jun 1990. This population of *C. cusickii* is unusual in containing many plants showing the pink to pink-purple bract coloration seen here. Also see Fig. 6.



Figure 6. Fasciated stem of *Castilleja cusickii*, Egger 322, WTU. The stem in this case was not significantly thickened, but the inflorescence was unique in the entire population.



Figure 7. *Castilleja foliolosa* showing thickened and flattened stem and expanded inflorescence. Bouverie Preserve, Sonoma Co., California, 4 Apr 2018. Photo by Richard Wasson, used with permission.



Figure 8. *Castilleja hispida* var. *hispida*, fasciated inflorescence, Anacortes Community Forest Lands, Skagit Co., Washington, 28 Apr 2007. Photo by Neil Gilham, used with permission.



Figure 9. Fasciated stem and inflorescence of *Castilleja indivisa*. Along County Rd 591, Brazoria Co., Texas, 17 Mar 2019. Photograph by Linda Leinen, used with permission.



Figure 10. Fasciated inflorescence (top) and stem (bottom) of *Castilleja indivisa*. Along County Rd 591, Brazoria Co., Texas, 17 Mar 2019. Photograph by Linda Leinen, used with permission.



Figure 11. *Castilleja linariifolia*, fasciated stem in center foreground, surrounded by typical stems. High ridge W of summit of Sheep's Knob, near gated road to summit, S of Gunnison River, Montrose Co., Colorado, 20 Jun 2008. Voucher: Egger 1457, WTU. Also see Fig. 12.



Figure 11. *Castilleja linariifolia*, fasciated stem. High ridge W of summit of Sheep's Knob, near gated road to summit, S of Gunnison River, Montrose Co., Colorado, 20 Jun 2008. Voucher: Egger 1457, WTU. Also see Fig. 12.



Figure 12. Stem fasciation in *Castilleja linariifolia*, Egger 1457, WTU.



Figure 13. *Castilleja miniata* var. *miniata*, Henderson 17711, OSC-ORE, showing stem fasciation in the central specimen, contrasting with the typical stems to each side. Note Henderson's hand-written annotation of the fasciated stem.



Figure 14. Stem fasciation in *Castilleja patriotica*, as seen in the left-most complete stem and in the stem fragment on the right of this isotype of the synonymous *C. blumeri*, Blumer 1380 (NY) and referred to by Standley (1909) and Holmgren (1976).



Figure 15. Two apparently partially fasciated stems of *Castilleja patriotica*, along Rustler's Park Rd, about 0.25 mi before cutoff to Barfoot Park, Chiricahua Mts., Chiricahua Co., Arizona, 26 Aug 1994. Near the type locality of the synonymous *C. blumeri*. Voucher: Egger 668, WTU. Also see Fig. 16.



Figure 16. Partially fasciated stem of *Castilleja patriotica*, Egger 668, WTU. Note that the proximal half of the stem is thickened, while the distal branches all emerge from the same point and are conspicuously narrower. This unusual morphology has only been noted in *C. patriotica* in a few plants from larger populations in the upper Chiricahua Mountains of Cochise County, Arizona.



Figure 17. Stem fasciation in *Castilleja purpurea*, example 1. Fallow field along US Hwy 67 just W of Bangs, Brown Co., Texas, 6 Apr 1990. Voucher: Egger 310, WTU. Also see Fig. 18.



Figure 18. Stem fasciation in *Castilleja purpurea*, example 1, Egger 310, WTU.



Figure 19. Stem fasciation in *Castilleja purpurea*, example 2. Fasciated stem on right, typical stem on left. Adjacent to US Hwy 377 ca. 25 mi NE of Brady, McCulloch Co., Texas, 20 Apr 1997. Voucher: Egger 855, WTU. Also see Fig. 21.



Figure 20. Stem fasciation in *Castilleja purpurea*, example 2. Inflorescence from fasciated plant. Adjacent to US Hwy 377 ca. 25 mi NE of Brady, McCulloch Co., Texas, 20 Apr 1997. Voucher: Egger 855, WTU. Also see Fig. 21.



Figure 21. Stem fasciation in *Castilleja purpurea* in plant on right, example 2, Egger 855, WTU.



Figure 22. *Castilleja stenophylla*, fasciated stem on right. SW of La Junta, Chihuahua, Mexico, 18 Aug 1998. Voucher: Egger 1044, WTU. Also see Fig. 23.



Figure 23. *Castilleja stenophylla*, fasciated stem on far right. Egger 1044, WTU.



Figure 24. *Castilleja wootonii*, fasciated main stem with unfasciated lateral branches. Along New Mexico Hwy 532 about 4 mi E of and below Sierra Blanca Ski Area, Sierra Blanca Range, Lincoln Co., New Mexico, 15 Jul 1989.



Figure 25. *Castilleja wootonii*, fasciated inflorescence. Along New Mexico Hwy 532 about 4 mi E of and below Sierra Blanca Ski Area, Sierra Blanca Range, Lincoln Co., New Mexico, 15 Jul 1989.

ACKNOWLEDGEMENTS

Thanks to Neil Gilham, Dave Hacker, Linda Lienen, Bodo Nuñez O., and Richard Wasson for permission to use their photographs. Thanks as well to the curatorial staff at ASC, NY, OSC, and WTU for assistance with specimens and images.

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