

THE IDENTITY AND STATUS OF *CASTILLEJA SUBALPINA* EASTWOOD AND *CASTILLEJA LONGIFLORA* KUNZE (OROBANCHACEAE)

J. MARK EGGER

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

ABSTRACT

The identity and status of *Castilleja subalpina* Eastw. are discussed and evaluated based on study of type material and recent field work in the vicinity of the type locality. It is now clear that the holotype is a unicate portion of a much larger, mixed collection and that *C. subalpina* belongs to sect. *Castilleja*, though whether it deserves formal nomenclatural recognition remains unresolved. The identity of the type collection of *C. longiflora* Kunze is also discussed, and previously unrecognized material likely from the type gathering is noted. Placement of *C. longiflora* in synonymy of *C. tenuiflora* Benth. is confirmed.

On 26 June 1894, Cyrus G. Pringle and his assistant John H. McGlashan set out from San Felipe del Agua, a community in the northern part of the city of Oaxaca, in the state of Oaxaca, Mexico. They “arose early to the enjoyment of a rainless day, a pleasant surprise” (Davis 1936) and ascended the nearby “Sierra de San Filipe,” also known as Cerro San Felipe, a portion of the range now known as the Sierra Juarez, eventually reaching the nearby summit, known as Peña de San Felipe. There they collected many specimens of a few species, as was Pringle’s habit, including a *Castilleja* species, the latter at 3140 meters elevation, not far below the summit at 3280 meters. These plants were later distributed by Pringle to at least 16 herbaria in Europe and North America as “*Castilleja scorzonerifolia* HBK.”

Fourteen years later, following the burning of her home herbarium at the California Academy of Science (CAS) in 1906, Alice Eastwood was working in Boston as a curatorial assistant at the Gray Herbarium (GH). During that time, she was able to study the large number of collections made by Pringle and others from Mexico and Central America. Having a particular interest in *Castilleja*, she subsequently published what is still the only revision of the entire genus for that region (Eastwood 1909). In this revision she described many new species of *Castilleja*, most of them still accepted as such today. Many of these new species were based on collections obtained by Pringle.

Among the new species published by Eastwood in her 1909 paper was *Castilleja subalpina* Eastw., based on the sheet of *Pringle 4722* at GH. The protologue for *C. subalpina* cites “*C.G. Pringle*, no. 4722 in part, distributed under *C. scorzonerifolia* HBK. (type in hb. Gray).” It is not clear how many or which other sheets of *Pringle 4722* she observed to conclude that only part of the collection represented her new species, and only the GH sheet bears her annotation as “*Castilleja subalpina*, n. sp.” It seems likely she may have seen those sheets present at BKL, NY, and/or US, as she spent time in New York and Washington, D.C., prior to reaching GH (Bonta 1991), but those sheets are unannotated by her. Following the publication of her 1909 revision, Eastwood visited BM, K and P, and during that time annotated the sheet of *Pringle 4722* at K-BENTH as “*Penstemon glandulosa* Greenman, Oct. 1911,” apparently an unconscious error intended as *Castilleja glandulosa* Greenman. This species, also described by Eastwood in her 1909 paper, is closely related to *C. scorzonerifolia*, but the specimens on all sheets of *Pringle 4722* except that at GH are clearly referable to the latter species. My herbarium and field studies in Mexico show *C. glandulosa* to be a separate but closely related species distinguished from *C. scorzonerifolia* by its usually more crisped-margined leaves, stipitate-glandular indument, and calyces with reddish to reddish-orange distal

coloration usually interrupted by distinctly yellow veins and lacking the distal ring of pilose hairs characteristic of most specimens of *C. scorzonerifolia*.

Eastwood's commentary notes that *Castilleja subalpina* "... belongs near *C. longiflora* Kunze [= *C. tenuiflora* Benth.] but has different pubescence and generally longer and narrower leaves" (see note below concerning *C. longiflora*, the type of which Eastwood apparently never saw). The key in Eastwood's monograph places *C. subalpina* closest to both *C. longiflora* and *C. auriculata* Eastw., the latter described by her in the same paper. Moreover, she placed *C. subalpina* in sect. *Hemichroma* Benth. (= sect. *Castilleja*), as opposed to her placement of *C. scorzonerifolia* in sect. *Euchroma*, based on the calyces cleft much more deeply abaxially than adaxially in the former, rather than the subequal abaxial and adaxial clefts of the latter. This is confirmed by the nature of the calyx incision visible in the GH sheet of *Pringle 4722* (Figs. 1-4) in contrast to the other sheets of that gathering (e.g., Figs. 7-8).

Subsequent to Eastwood's revision, there is little mention of *Castilleja subalpina* in the botanical literature except on floristic or phylogenetic lists of accepted species (e.g., Méndez-Larios & Hernández 1992; Tank et al. 2009; Villaseñor 2016; International Plant Name Index 2022), though it is absent from others (e.g., Méndez-Larios & Villaseñor 2001). Other treatments of the *Castilleja* species of Mexico have mostly consisted of descriptions of new species (e.g., Nesom 1992a; Egger 2002b; Medina & Carranza 2017), treatments of species occurring in regions other than Oaxaca (e.g., Holmgren 1976; Egger 1992a; Egger et al. 2022), treatments of specific species groups (e.g., Nesom 1992b, 1992c), or specialized treatments not involving all species (e.g., Chuang & Heckard 1993). The one exception to this trend was a brief comment concerning *C. subalpina* by Nesom (1992c), in which he excluded this species from the complex of species informally described as the *Castilleja tenuiflora* Group (the subject of his paper and the associated key), named for the widespread species *C. tenuiflora* Benth. This assemblage is a portion of the broader sect. *Castilleja*, as defined by Holmgren (1976) as the "Tenuiflorae Group," and part of the broader subg. *Castilleja*. Concerning *C. subalpina*, Nesom stated that "Eastwood (1909) regarded *Castilleja subalpina* Eastw. as most similar to the species of sect. *Castilleja*, but the plants of the holotype (GH) clearly belong instead with the taxa centered around *C. scorzonerifolia* Kunth (sect. *Euchroma* (Nutt.) Benth.)"

On 25 August 2001, I visited the slopes of Cerro San Felipe, specifically to look for plants resembling Eastwood's type of *Castilleja subalpina*, but I was unable to reach the precise vicinity of the summit due to weather and time constraints. I did reach near the summit of an adjacent peak, Corral de Piedra, at a similar elevation but about 4 km along a ridge east-northeast of where *Pringle 4722* was obtained. I did find a number of plants of *C. scorzonerifolia* but nothing that resembled the two stems on the holotype sheet. While I was unable to obtain photos of the live plants, I did collect a few specimens as *Egger 1203*, WTU (Fig. 9).

More than two decades later, Oaxacan botanist, Eugenio Padilla climbed to the summit area of Cerro Peña de San Felipe and photographed a plant that appears to be the same species as that described by Eastwood and closely resembling the GH sheet of *Pringle 4722*. Padilla then posted his photo on the Naturalista website, <<https://www.inaturalist.org/observations/127010431>> (accessed 8 Feb 2023), where I recognized it as likely the same species as Eastwood's *Castilleja subalpina* (Figs 5-6). The location of this new record makes it essentially a topotype, being close to the summit of the mountain and at an elevation of 3195 meters, while *Pringle 4722* was collected at about 3140 meters.

I have verified the presence and identity of sheets of *Pringle 4722* in the following herbaria: BKL[2], CM, E, GH, HBK, JE, K-BENTH, KFTA, M, MEXU, MO, NDG, NY[2], S, US, and WIS. Of these 18 sheets, 17 contain only plants readily assignable to the name under which they were distributed, *Castilleja scorzonerifolia*. However, as Eastwood astutely observed, the two stems found on the GH sheet do not correspond to that species in several characters of the inflorescence. The

calyces are cleft far more deeply abaxially than adaxially and lack the upper medial band of long, whitish hairs, the corolla beak is longer and more exerted, and the floral bracts are lanceolate and narrowing distally to an acute tip (Figs. 1-6 vs. Figs. 7-11). Consequently, the name *C. subalpina* should be applied only to the GH sheet:

Castilleja subalpina Eastwood, Proc. Amer. Acad. Arts 44: 584. 1909. **TYPE: México. Oaxaca.**
Sierra de San Felipe [= Cerro San Felipe, part of the Sierra Juarez] altitude 3140 m, 26 Jun 1894,
C.G. Pringle 4722 in part, distributed as *C. scorzonerifolia* HBK. (holotype: GH).

While it is now clear that Eastwood's conception of *Castilleja subalpina* as a unique portion of *Pringle 4722*, belonging to "sect. *Hemichroma*" (= sect. *Castilleja*) rather than to sect. *Euchroma* is correct, its status as an accepted species or a synonymous name remains unresolved. Among the presently accepted *Castilleja* species occurring in Oaxaca, it most closely resembles *C. auriculata* and *C. tenuiflora*, the typical varieties of which are both moderately common in the mountainous regions of the state, including in the Sierra Juarez. Eastwood's diagnosis of *C. subalpina* is uncharacteristically vague and non-diagnostic, while her key is not strictly parallel and is partly contradicted in her formal description of the species. In her key, Eastwood distinguished *C. subalpina* from its putatively closest relatives, paraphrased as follows:

- c. Pubescentia dense canescens et minute glandulosa, caulibus idem pilosis
..... **C. auriculata** [and] **C. longiflora**.
- c. Pubescentia divaricate pilosa et scabrido-puberula. Folia viridia lanceolata. Flores suberecti
..... **C. subalpina**
- c. Pubescentia plerumque adpressis et scabrido-puberula. Flores divaricati
..... **C. tenuiflora** [and] **C. canescens**

Eastwood's Latin description, however, characterizes the pubescence of the herbage as "sparse pilosis et dense scabrido-puberulis et obscure glandulosis," partially contradicting her key. Moreover, the leaf coloration and flower orientation are both widely variable with age and other factors in most species of the Tenuiflora Group. Among the presently accepted forms, *C. auriculata* var. *auriculata* is readily distinguished from the typical form of *C. tenuiflora* by its densely ranked and strongly auriculate leaves, as well as by the presence of many stipitate-glandular hairs in the indument. The leaves of *C. tenuiflora* are more sparsely ranked and only inconspicuously auriculate, and the indument of the herbage generally lacks stipitate-glandular hairs. In some respects, the type of *C. subalpina* and the apparent topotype specimen appear to be intermediate in terms of the ranking and proximal structure of the leaves. The pubescence of the stems and leaves (Figs. 2-4) is also apparently intermediate, being, in Eastwood's words "sparsely pilose and densely scabrid-puberulent and obscurely glandular." The ambiguity of the traits visible in these plants indicates the need for additional field work in the vicinity of the type locality. It may be that *C. subalpina* is a rare, higher elevation, endemic derivative from the Tenuiflora Group. It is also possible that these plants are simply atypical variants of one of the two closely related species occurring in that region or that they express evidence of genetic introgression between them.

Finally, in her 1909 revision, Eastwood accepted *Castilleja longiflora* as a unique species in the Tenuiflora Group, though she merely quoted Kunze's description and cited only collections unassociated with the type gathering by Ehrenberg, which she apparently never saw. Holmgren (1976) did not include any mention of this entity, perhaps because of the lack of verifiable type material. He also did not include any discussion of *C. subalpina*, though in 1971 he did annotate one of the sheets of *Pringle 4722* at NY — "This sheet probably does not have any isotype material on it." This implies he was aware of the differences between Eastwood's GH sheet and NY sheet. Nesom (1992c) reduced *C. longiflora* to synonymy under *C. tenuiflora*, based on the description given in the protologue and in the notes provided by Bentham (in DC., Prodr. 10: 533, 1846), wherein

the latter author indicated he viewed the Ehrenberg collection. However, no such specimen is now present at K or K-HOOK. Kunze (1842) in his description of *C. longiflora* cited only Ehrenberg's collection and provided no number, date, or specific location, mentioning only that the specimens were grown from seed collected in the "regione frigida" of Mexico. It is unclear whether the seeds were cultivated by Ehrenberg or by Kunze, but apparently any specimens of these plants at both B and Kunze's herbarium at LZ were destroyed by bombing of Berlin and Leipzig in World War 2.

Subsequently, in 1992-3, I received a loan of many *Castilleja* collections from LY-GAN. Most of these collections were unmounted and still in their original papers, some dating to the 1800's. Among them, I identified over 40 type collections, most of them isotypes from widely distributed collections, such as those of C.G. Pringle. Among them, however, was an unmounted sleeve containing a collection by Ehrenberg from Mexico, dated 1839 and identified as "*Castilleja tenuiflora* Bth." The printed portion of the label reads "Ex Museo botanico Berolinensi." It seems highly likely that Ehrenberg sent a portion of his plants to Gandoger, who also signed the label, in addition to the material sent to Kunze, who subsequently described it as *C. longiflora* in 1842. While the line connecting the sheet at LY-GAN is not thoroughly established, it seems reasonable to assume that the sheet in question represents the only extant material from the collection Kunze used to describe his new species. In any case, I agree with Nesom's conclusion that *C. longiflora* should be considered as synonymous with *C. tenuiflora*, based on both the original description and its concordance with the sheet present at LY-GAN. With the permission of the LY staff, we mounted the stems and affixed the original label, and the images seen below (Figs. 12-14) were obtained at WTU in March 1994, prior to returning the sheet to LY. No other images of it are available on the internet at present.

ACKNOWLEDGEMENTS

Thanks to the curatorial staff of the numerous herbaria cited above for their assistance in my studies of type specimens of *Castilleja*, including imaging and assistance with loans, and especially to Anthony R. Brach (GH) for the high-resolution images of the holotype of *C. subalpina*. I am also very grateful to Eugenio Padilla for the use of his photo from the type locality.

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Figure 1. Holotype of *Castilleja subalpina* Eastw., Pringle 4722 (GH).



Figure 2. Holotype of *Castilleja subalpina* Eastw., Pringle 4722 (GH). Crop of left inflorescence. Note the deep abaxial calyx cleft and the relatively long corolla beak, as well as the narrowing, acute-tipped distal portion of the bracts.



Figure 3. Holotype of *Castilleja subalpina* Eastw., Pringle 4722 (GH). Crop of right inflorescence.



Figure 4. Holotype of *Castilleja subalpina* Eastw., Pringle 4722 (GH). Crop of middle stem and indument.



Figure 5. *Castilleja subalpina*, putative topotype, Cerro Peña de San Felipe, Oaxaca, Mexico, 16 July 2022. Photo by Eugenio Padilla, used with permission.



Figure 6. *Castilleja subalpina*, composite image of live plant (16 July 2022) and a portion of the holotype collected 26 June 1894 (GH). Live plant photo by Eugenio Padilla, used with permission.



Figure 7. Putative isotype of *Castilleja subalpina* Eastw., Pringle 4722 (WIS). This sheet contains only stems of *C. scorzoneraefolia* Kunth and is very typical of all the remaining sheets of Pringle 4722 apart from the single sheet at GH.



Figure 8. Crop of lower portion of putative isotype of *Castilleja subalpina* Eastw., Pringle 4722 (WIS), showing three typical stems of the widespread Mexican species *C. scorzonerifolia*.



Figure 9. *Castilleja scorzonerifolia*, near summit of Corral de Piedra, Sierra Juarez, Oaxaca, Mexico, 25 August 2021, Egger 1203 (WTU). This site is about 4 km from the collection site of *Pringle* 4722.

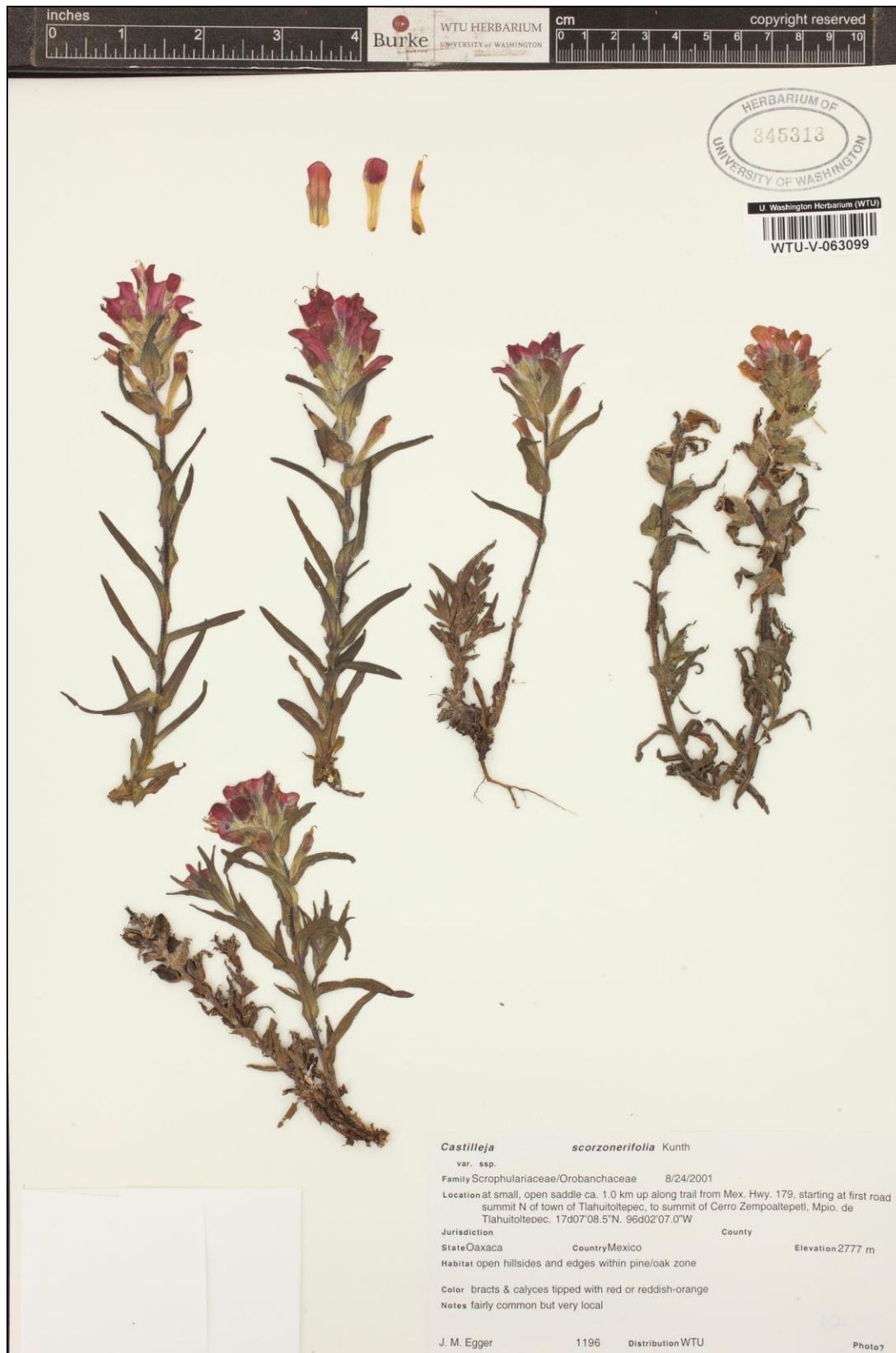


Figure 10. Typical *Castilleja scorzonerifolia* Kunth, upper middle slopes of Cerro Zempoaltepetl, Oaxaca, Mexico, 24 August 2001, Egger 1196 (WTU). Also see Fig. 11 from same population.



Figure 11. Typical *Castilleja scorzonerifolia* Kunth, upper middle slopes of Cerro Zempoaltepetl, Oaxaca, Mexico, 24 August 2001. Subsequently collected as *Egger 1196* (WTU). Photo by Egger.



Figure 12. Ehrenberg s.n., apparent type material of *Castilleja longiflora* Kunze (LY-GAN), after mounting on herbarium paper at WTU in early 1993, prior to its return to LY.



Figure 13. *Ehrenberg s.n.*, apparent type material of *Castilleja longiflora* Kunze (LY-GAN), loose stems in paper sleeve, as received on loan at WTU from LY-GAN in late 1992.

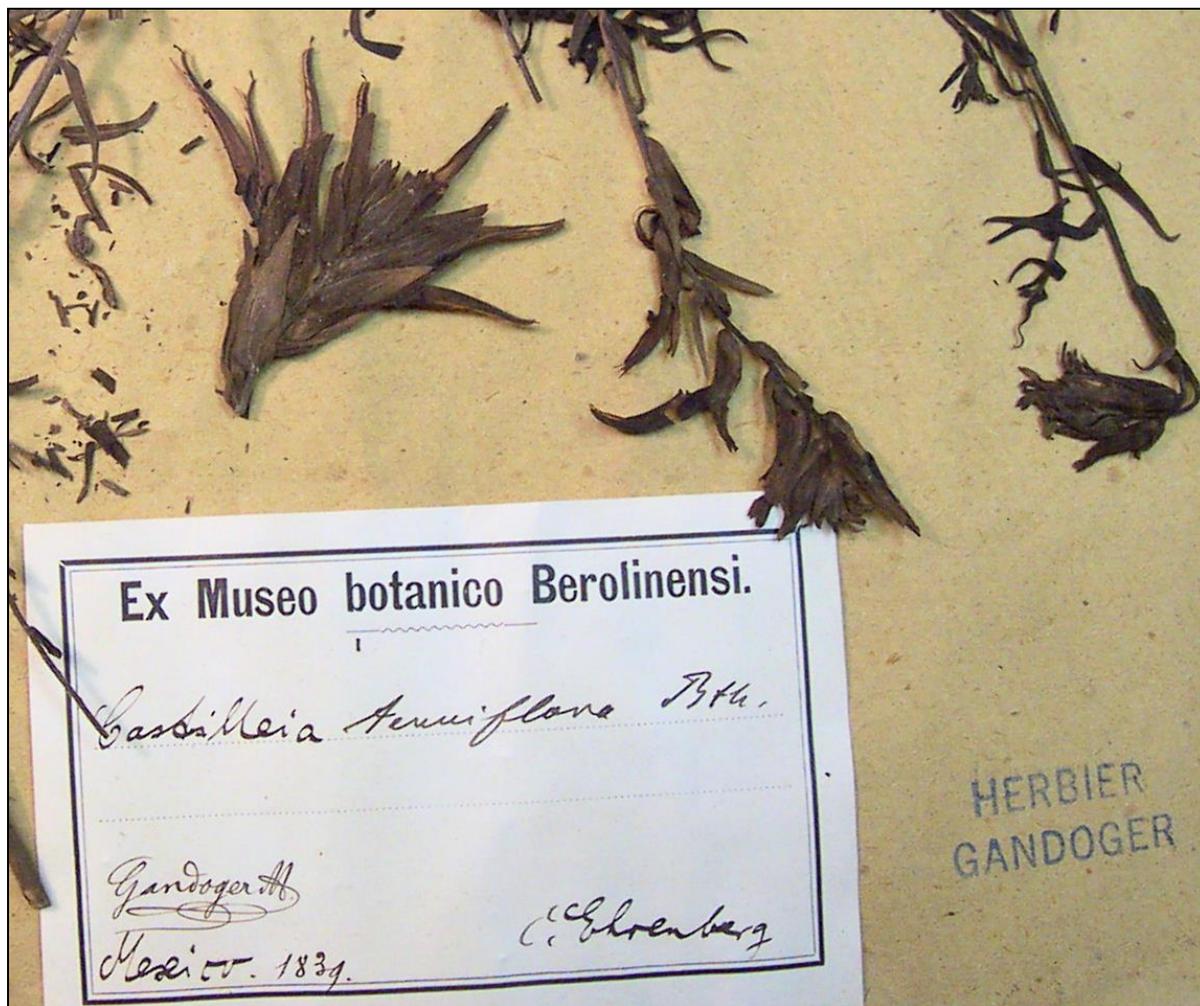


Figure 14. *Ehrenberg s.n.*, apparent type material of *Castilleja longiflora* Kunze (LY-GAN), loose stems and original label from B in paper sleeve, as received on loan at WTU from LY-GAN in late 1992.